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From Somatic Growth to Community Structure of Marine Fishes: Explaining Variation with Physical Drivers and Methodological Biases at Multiple Scales

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From Somatic Growth to Community Structure of Marine Fishes: Explaining Variation with Physical Drivers and Methodological Biases at Multiple Scales

by

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Dedication

To Angelina, Tucker, and Copper. "*Tell me, what is my life without your love"* – George Harrison.

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Abstract

From Somatic Growth to Community Structure of Marine Fishes: Explaining Variation with Physical Drivers and Methodological Biases at Multiple Scales

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The University of Texas at Austin, 2021

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The life history traits, population dynamics, and community ecology of marine fishes vary along spatio-temporal gradients in environmental conditions and habitat (i.e. physical conditions). Accordingly, incorporating physical drivers into fisheries assessments can improve fishery management advice, and thus the sustainability of fisheries. However, collective inferences on the effects that physical conditions have on fishes can be difficult to draw due to confounding effects of scale, sampling procedure, gear type, and other aspects of methodology. Here, I examined the role of physical drivers and methodological biases in explaining variation in aspects of fish populations and communities across levels of biotic organization. In the first study contained in this dissertation, I employed simulations to demonstrate the influence of sample distribution on growth parameter estimates and per-recruit assessment for the Gulf Corvina (*Cynoscion othonopterus*) in the Gulf of California. Sample distribution could confound growth parameter estimates in conventional assessments, and is especially important to account for when documenting spatio-temporal variation in growth, as sample distributions are

rarely consistent over time and space. In the second, I described the effects – or lack thereof – of physical conditions on the distributions of common petroleum platform-associated fish species in the Gulf of Mexico through large-scale submersible camera sampling. In the third, I combined camera and hydroacoustic data to characterize water-column fish communities at petroleum platforms and identified the dominant physical drivers that shape them. In the fourth, I examined the challenges of assessing fish community size spectra with hydroacoustics in rugose marine habitats. Assessing the size spectra of fish communities over time and space is useful for understanding the effects of physical conditions and anthropogenic activities on community structure, and using hydroacoustic technology allows size spectra to be assessed more rapidly and efficiently than conventional methods. The findings and approaches described in this dissertation may be used to understand variation in fish growth, distribution, abundance, and community structure in response to physical drivers, thereby making spatial and ecosystem considerations more accessible to fisheries assessment and management frameworks.

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Chapter 1: Introduction

A key tenant of ecology is that the biological traits and interactions of individuals scale up to influence population and community dynamics (Cody et al. 1975; Brown et al. 2004; Vellend 2010; Bolnick et al. 2011; Secor 2015). For marine fishes, basic biological characteristics termed 'life history traits' (e.g. growth rate, maximum length, age-at-maturity, longevity, etc.) determine population demographic characteristics (Cole 1954; King and McFarlane 2003; Roos et al. 2003; Bjørkvoll et al. 2012; Kindsvater et al. 2016). Accordingly, most fisheries stock assessments are built upon a foundation of life history traits and incorporate the population processes that result from those characteristics (Punt and Hilborn 1997; Maunder and Punt 2013; Hilborn and Walters 2013).

A challenge facing modern fisheries assessments is that the life history traits, population processes, and community dynamics of marine fishes vary over time and space (Ciannelli et al. 2008; Guan et al. 2013; Berger et al. 2017). Certain life history traits of fishes are influenced by environmental conditions (Conover and Present 1990; Ricklefs and Wikelski 2002; Ohlberger 2013) and habitat characteristics (Winemiller 1989; Schlosser 1990; Vila-Gispert et al. 2002) (hereafter referred to as 'physical conditions'), as well as density-dependent processes (Fowler 1981; Rose et al. 2001; Lorenzen and Enberg 2002). Each of these also affects interactions between individuals (Crowder and Cooper 1982; Hixon and Carr 1997; Pörtner and Farrell 2008). Species distributions are therefore determined through a combination of environmental filtering and ecological processes (Leibold et al. 2004; Kraft et al. 2015; Cadotte and Tucker 2017). A confluence of biophysical influences on species distributions and random processes (e.g. ecological drift) results in the organization of a fish community in a particular area (Ricklefs 1987; Hubbell 2001; Cavender-Bares et al. 2009), which may persist in a consistent form or not depending on its organization and the influence of natural and anthropogenic forces (Jennings et al. 1995; Anderson and Piatt 1999; Litzow and Ciannelli 2007). Thus, to provide accurate fisheries management advice, understanding the effects of physical conditions on individuals, populations,

and communities is essential (Dickey-Collas et al. 2010; Zwolinski and Demer 2012; Skern-Mauritzen et al. 2016).

Accordingly, progress has been made towards incorporating physical drivers into fisheries assessments. In ecosystem-based fisheries management (EBFM), ecological interactions, community dynamics, and socioeconomic factors are integrated with population processes and life history traits in the context of the physical conditions that affect them all (NRC et al. 1999; Pikitch et al. 2004; Link 2010). Though EBFM has been implemented in some cases (e.g. Hawaiian coral reefs, Alaskan scallops, Northeast Atlantic groundfish; Trochta et al. 2018), advances have largely been academic (Skern-Mauritzen et al. 2016). While EBFM has been difficult to implement in practice, spatial dynamics in parameters and stock structure are more commonly incorporated into modern assessments (e.g. North American Pacific Halibut, Antarctic Toothfish, Canary Rockfish; Berger et al. 2017; Punt 2019). Ultimately, these dynamics are driven by variation in physical conditions (Goethel et al. 2011; Berger et al. 2017; Punt 2019).

Variability in methodology and scale may confound collective inferences on the effects of physical conditions, comparisons between studies, and integration of data from multiple sources (Levin 1992; Link et al. 2010; Hobday and Evans 2013). However, some fishery-independent data collection approaches can minimize the confounding effects of methodology. For example, active acoustic technologies are often paired with other gears, such as underwater cameras or trawls, in order to evaluate biases and gain a more complete understanding of fish populations and communities than could be obtained with one gear type alone (McClatchie et al. 2000; Simmonds and MacLennan 2008; Murphy and Jenkins 2010). Researchers do not have the ability to directly minimize biases in fishery-dependent data, although simulations may be used for quantifying variability and the impact of different sampling outcomes at each step of the process (e.g. Gwinn et al. 2010; Rose et al. 2017; Thorson et al. 2020). Regardless of the source of the data, modern stock assessments rely on the quantification of uncertainty (Privitera-Johnson and Punt 2020). Accordingly, sources of variation in a metric – methodological, physical, or otherwise – must be quantified prior to its incorporation into formal stock assessment and management frameworks.

Quantifying sources of variation in fisheries assessment inputs is particularly important in data-poor assessments, which are directly tied to life history traits in relatively simple frameworks due to the typical lack of reliable exploitation data (Porch et al. 2006; Edwards et al. 2012; Chrysafi and Kuparinen 2015). Fisheries in the Gulf of California, Mexico, (GOC) are assessed with such methods. For the Gulf Corvina (*Cynoscion othonopterus*), persistent exploitation with highly-selective gear has severely truncated the size and age structure of the population (Erisman et al. 2014; Ortiz et al. 2016), which may confound estimates of the life history parameters used in fisheries assessments. Indeed, multiple studies employing different datasets have reached different conclusions regarding the growth of the species in every aspect, from specific growth parameters to general growth pattern (Gherard et al. 2013; Aragon-Noriega 2014; Mendoza et al. 2017). For fisheries assessments to provide accurate management advice for the Gulf Corvina, the source of this discrepancy must be identified and resolved. Accordingly, I investigated the impact of sample distribution on growth parameter estimates and per-recruit assessments for the Gulf Corvina (Chapter 2). I fitted a variety of somatic growth models to raw data collected by multiple means and to data from a simulated ideal sampling scenario. Then, I fitted yield and spawning stock biomass per-recruit models to demonstrate the impact of incorrectly specifying growth parameters on stock status estimates. This effort is not only crucial for the conservation of this highly-exploited species, but also for the economic wellbeing and food security of the coastal communities that depend on Gulf Corvina. Further, the approach taken in Chapter 2 may be applied beyond the Gulf Corvina example, and is particularly relevant to studies describing spatio-temporal variation in growth driven by physical conditions.

In contrast to the GOC, fish stocks in the U.S. Gulf of Mexico (GOM) are assessed and managed using state-of-the-art methods. For many exploited reef-associated fishes in the GOM, extensive fishery-independent sampling programs are used to estimate biological characteristics and stock abundance (e.g. Southeast Area Monitoring and Assessment Program). These programs are highly-effective for monitoring fishes in the low-profile outcroppings that characterize natural reef habitat in the GOM, yet they have not yet been optimized for sampling the largest and most

complex of reef habitats: petroleum platforms. Thousands of petroleum-associated structures are found throughout the GOM (BOEM 2019). They provide valuable habitat for a great diversity of reef fishes and are important for the GOM's fisheries, although estimates of their exact contribution to GOM-wide fish stocks vary depending on the methodology used to provide estimates (e.g. Red Snapper *Lutjanus campechanus,* Gallaway et al. 2009; Karnauskas et al. 2017). However, there has been a net loss of platforms over the last decade in the GOM (BOEM 2019; Munnelly et al. 2020), and climate change is expected to substantially alter the physical conditions fishes are exposed to at platforms (Justić et al. 1996; Karnauskas et al. 2015; Laurent et al. 2018). Fisheries assessments with spatial and ecosystem considerations are best suited for incorporating the effects of these phenomena, and indeed, some GOM stock assessments consider the spatial structure of the stock (e.g. Red Snapper; Southeast Data Assessment and Review (SEDAR) 2018).

Including spatial and ecosystem considerations into fisheries assessments requires knowledge of the distribution of a species, and how it might change. Some species may shift their distributions in response to changes in physical conditions, yet others may develop physiological or behavioral adaptations (Rijnsdorp et al. 2009; Secor 2015; Habary et al. 2017). The productivity of a stock, and thus the level of exploitation it can sustain, may be affected in either case. Accordingly, I examined the role of physical conditions in structuring the water-column and biogeographic distributions of common marine fish species at petroleum platforms in the GOM (Chapter 3). Although prior studies have described variation in fish assemblages and distributions at platforms (e.g. Gallaway and Lewbel 1982; Stanley and Wilson 2004; Munnelly et al. 2019), inferences were often based on data collected in a specific region or relatively limited number of study sites. The effect of scale is well-known in ecological studies (Levin 1992), so in order to separate the effects of physical conditions from artifacts of scale, I collected the data for Chapter 3 throughout the GOM. In addition to building upon the conclusions of previous studies at a larger scale, I examined the distributions of several common platform-associated species for which there is no published literature.

Assessing the impacts of physical conditions on fishes using only one gear type can mask methodological biases, regardless of the scale of the approach. In order to gain a more complete understanding of platform-associated fish communities (Chapter 4), I examined multiple community metrics collected with camera and acoustic data at the platforms studied in Chapter 3. This 'optic-acoustic' approach has been increasingly advocated for assessing fish populations and communities (Demer et al. 2009, 2020; Michaels et al. 2019), as the two gear types complement one another due to substantial differences in selectivity and sources of bias, resulting in a complete and robust description of the fish community being sampled. By examining a variety of metrics with this approach, it was possible to identify the dominant physical drivers that shape platform-associated fish communities, as well as areas in which changes in physical conditions might be most impactful.

Extensive fishery-independent sampling programs and spatially-resolved assessment methods are necessary for providing fishery management advice in dynamic environments. However, extensive, large-scale sampling programs and assessments cannot be conducted frequently due to their demand on resources. Thus, it is useful to develop indicators in which the effects of physical conditions on fish populations and communities can be monitored rapidly and efficiently. Assessing the size spectrum of a fish population or community can be a useful way to understand the effects of physical and biological stressors (Wilson et al. 2010; Blanchard et al. 2017; Heneghan et al. 2019). Conventional methods are time and labor-intensive, but hydroacoustic data may be collected rapidly and efficiently over wide spatial and temporal scales. In order to facilitate the widespread use of size spectra assessment as an indicator of changes in fish community structure, I quantitatively assessed the challenges associated with assessing size spectra with hydroacoustic technology in a rugose marine habitat (Chapter 5). Additionally, I determined the conditions in which acoustic size spectrum slopes may be compared with those derived from other methods. Though developed using data collected at petroleum platforms in the GOM, this approach is generally applicable to a variety of marine habitats – including to document further length truncation in the Gulf Corvina stock (Chapter 2).

The studies contained in this dissertation examined the degree to which physical conditions and methodological biases may be assoicated with variation in fish populations and communities. Physical and methodological influences affect the estimation of parameters from individual to community-wide scales. Separating one from the other is crucial for ensuring that unbiased data are used to draw scientific inferences and inform fisheries assessments. Quantifying and partitioning these effects facilitates the incorporation of spatial and ecosystem considerations into fisheries assessments and management, which may help to sustain fisheries in dynamic environments.

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Chapter 2: The influence of sample distribution on growth model output for a highly-exploited marine fish, the Gulf Corvina (*Cynoscion othonopterus*) [1]

ABSTRACT

Estimating the growth of fishes is critical to understanding their life history and conducting fisheries assessments. It is imperative to sufficiently sample each size and age class of fishes to construct models that accurately reflect biological growth patterns, but this may be a challenging endeavor for highly-exploited species in which older fish are rare. Here, we use the Gulf Corvina (*Cynoscion othonopterus*), a vulnerable marine fish that has been persistently overfished for two decades, as a model species to compare the performance of several growth models. We fit the von Bertalanffy, Gompertz, logistic, Schnute, and Schnute-Richards growth models to length-at-age data by nonlinear least squares regression and used simple indicators to reveal biased data and ensure our results were biologically feasible. We then explored the consequences of selecting a biased growth model with a per-recruit model that estimated female spawning-stock-biomass-per-recruit and yield-per-recruit. Based on statistics alone, we found that the Schnute-Richards model described our data best. However, it was evident that our data were biased by a bimodal distribution of samples and underrepresentation of large, old individuals, so we found the Schnute-Richards model output to be biologically implausible. By simulating an equal distribution of samples across all age classes, we found that sample distribution distinctly influenced model output for all growth models tested. Consequently, we determined that the growth pattern of the Gulf Corvina was best described by the von Bertalanffy growth model, which was the most robust to biased data, comparable across studies, and statistically comparable to the Schnute-Richards model. Growth

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model selection had important consequences for assessment, as the per-recruit model employing the Schnute-Richards model fit to raw data predicted the stock to be in a much healthier state than per-recruit models employing other growth models. Our results serve as a reminder of the importance of complete sampling of all size and age classes when possible, and transparent identification of biased data when complete sampling is not possible.

INTRODUCTION

Age and size data inform estimates of life history parameters that are crucial to fisheries stock assessments. In early assessments such as Beverton and Holt's yield-per-recruit model (1957), size at age was critical for estimating reproductive output and thus the sustainability of fisheries. In today's age-structured stock assessments, size at age is used to convert from biomass to number of fish, determine selectivity, and calculate expected length compositions (Francis, 2016). Similarly, size (i.e., length or weight) at age is used in size-structured stock assessment models to inform transitions between size bins and determine length composition (Punt et al., 2016). Accurately representing the relationship between size and age is particularly important for vulnerable fish and in data-poor fisheries, in which life-history parameters and population structure often drive stock assessments and management decisions (Dulvy et al., 2004; Froese, 2004; Honey et al., 2010; Hordyk et al., 2016). Specifically, these types of assessments rely heavily on age-length data to confer insights on vulnerability and overfishing (Erisman et al., 2014).

When modelling the relationship between age and size for the purposes of assessment, and for any purpose, each age and size class must be sufficiently represented to generate growth parameters that reflect biological growth (Cailliet et al., 1986; Cailliet and Tanaka, 1990; Francis and Francis, 1992; Cailliet and Goldman, 2004). It is important to make the distinction between this type of sampling and sampling to reflect population structure, which should not be the goal of age and growth studies as this reflects bias due to the relative scarcity of large and old individuals. Sufficiently representing each size and age class may be especially difficult in highly-exploited species, as exploitation alters the population structure of fishes by preferentially selecting for large

and old fish individuals (Mason, 1998; Berkeley et al., 2004). The ramifications for failing to acknowledge selection are clear, as length-selective fishing mortality distorts growth curves (Walker et al., 1998). Further, the lack of representation of large and old individuals could result in underestimation of lifespan and longevity, which makes fishery management measures less effective (Campana, 2001; Cailliet and Andrews, 2008; Goldman et al., 2012). Large and old fish drive estimates of the maximum average length parameter L_∞, and without them, L_∞ is underestimated and the growth rate (typically denoted by K) is overestimated. The underestimation of L_∞ and the overestimation of K lead to the assumptions of a shorter generation time and less mortality, and thus more resiliency to high levels of fishing pressure (Campana, 2001; Goldman et al., 2012; Harry, 2017). The L_∞ term is particularly important when growth models are incorporated into stock assessment (Wells et al., 2013). This problem may also occur in growth modelling for vulnerable fish or in data-poor fisheries, where lack of representation of each age and size class due to sampling constraints or the scarcity of individuals may similarly affect parameter estimates. Fishery dependent data are often the only data available for growth modelling, which may be acceptable only as long as the inherent biases and limitations are acknowledged.

Several models have been developed to quantify the relationship between age and size, with body length being the most common metric of size. Typically, asymptotic growth models are used to quantify this relationship. These models describe fast growth rate in the earliest years of life and slower growth in later years. Despite some criticism (Roff, 1980; Czarnołe‘ski and Kozlowski, 1998), the most widely used is the von Bertalanffy growth model (Chen et al., 1992; Kimura, 2008). Rooted in bioenergetics, this model is intended to give a biologically relevant representation of how catabolic and anabolic processes work within a fish to change growth over the lifespan of fishes (von Bertalanffy, 1938; Pauly, 2010). Over the years, there have been many re-parameterizations of von Bertalanffy with incorporation of growth-influencing factors and applications to a variety of situations (Gallucci II and Quinn, 1979; Ratkowsky, 1986; Helser and Lai, 2004; Kimura, 2008; Brunel and Dickey-Collas, 2010; van Poorten and Walters, 2016), but

the original parametrization is still the most commonly used (Lorenzen, 2016). Other asymptotic growth models are commonly used in fisheries, such as the Gompertz growth model (Gompertz, 1825) and the logistic growth model (Ricker, 1975).

In recent years, fish growth models have moved from a foundation in bioenergetics to being more statistically driven (van Poorten and Walters, 2016). These models are inherently more flexible, allowing them to capture subtleties in growth patterns that may not be captured by the more inflexible growth models. The Schnute model (Schnute, 1981), for example, has four curve families that the model may assume based on which types of data the model is fit to and what other functions are incorporated into the framework. Another flexible growth model, the Schnute-Richards model (Schnute and Richards, 1990), can describe biphasic growth among several other forms. By design, the Schnute-Richards model may be equivalent to the other growth models discussed above when the proper values are specified for its dimensionless parameters. Fish growth is inherently plastic and fish do not all grow the same way (Weatherley, 1990; Lorenzen, 2016), so a flexible growth model may be advantageous in certain situations. However, these flexible models may also be more sensitive to sampling biases in data, potentially producing growth patterns that reflect the size-frequency distribution of fish collected rather than the biological growth pattern of the species.

The Gulf Corvina *(Cynoscion othonopterus)* is an ideal species to examine the performance of multiple growth models in a vulnerable marine fish. Endemic to the northern Gulf of California, Mexico (Robertson and Allen, 2008), it is currently listed as vulnerable under the International Union for the Conservation of Nature (IUCN) Redlist (Chao et al., 2016). Gulf Corvina have experienced persistent overfishing on their spawning aggregations for the past two decades, which have resulted in growing concern for the fishery's stability and longevity (Erisman et al., 2012; Ruelas-Peña et al., 2013; Erisman et al., 2014; Ortiz et al., 2016). The life history of this species has been well documented and provides an ideal foundation for future analysis of individual and population growth (Román-Rodriguez, 2000; Gherard et al., 2013. With a documented maximum size of 1013 mm total length (TL) and a documented maximum age of 9 years, Gulf Corvina is a

fast growing, short lived species which reaches sexual maturity at 2 years of age (Gherard et al., 2013). However, the combination of highly efficient, size-selective gear and persistent overfishing have severely truncated the age structure of the population (Erisman et al., 2014; Ortiz et al., 2016). The mean age of capture of Gulf Corvina is 5 years (*ca.* 700 mm TL), and few individuals older than age 7 or younger than age 4 have been observed in the fishery (Gherard et al., 2013; Erisman et al., 2014; Ortiz et al., 2016).

Past studies of Gulf Corvina growth, which have relied solely on fishery-dependent data with incomplete sampling of all size and age classes, have produced different results due to differences in model selection approach. Based on the congruence of the model with the growth pattern of many species of the genus *Cynoscion* and other sciaenid fishes (Rutherford et al., 1982; Lowerre-Barbieri et al., 1995; Rodriguez and Hammann, 1997), Gherard et al. (2013) took a conservative, single model approach and fit the von Bertalanffy growth model to Gulf Corvina age-length data. Conversely, Aragón-Noriega (2014) chose a statistically-driven approach and fit several models to multiple datasets, concluding that Gulf Corvina grew in a biphasic pattern with slow growth in the beginning of life, rapid growth after age two, and slow growth after age four. Notably, Aragón-Noriega's (2014) estimates for the L_∞ parameter varied greatly, from 735.0 to 1126.6 mm, depending on which dataset was used. Given this variability, absence of biphasic growth patterns in similar sciaenids, and the distance from the maximum observed length of Gulf Corvina (1013 mm; Gherard et al., 2013), Aragón-Noriega's (2014) estimates may be biologically unrealistic. Mendivil-Mendoza et al. (2017) took a similar approach and found a similarly wide range of L_∞ values (666.7 – 1306.0 mm). However, despite fitting models to similar data and selecting the same model as Aragón-Noriega (2014), Mendivil-Mendoza et al. (2017) did not describe the biphasic growth pattern recorded by Aragón-Noriega (2014). The existence of discrepancies between the previous Gulf Corvina growth studies and the importance of the age-length relationship to the stock assessment of the fishery merit further investigation on the growth pattern of the species.

Here, we model the growth of Gulf Corvina and draw conclusions about data needs and fisheries assessments. Our specific objectives were to: (1) assess how representation of size and age classes affected growth parameter estimates and (2) compare the performance of multiple growth models for describing age-at-length data for Gulf Corvina. Through generating a more complete dataset than previous studies and testing for biases in our data with simple indicators, we addressed these objectives. Moreover, using the results of simulations with a per-recruit model, we discussed the implications of misrepresenting growth in highly-exploited, vulnerable marine fishes.

MATERIALS AND METHODS

Data Collection

Seven hundred and forty-nine Gulf Corvina were sampled from 2009 through 2013 at the three locations in the upper Gulf of California: El Golfo de Santa Clara (Sonora), San Felipe (Baja California), and El Zanjón (Baja California). Information on total length (TL) was recorded to the nearest mm for each fish collected, and the sagittal otoliths were removed, dried whole and stored until further use. Five hundred and thirty of these samples were collected from the commercial Gulf Corvina fishery and from bycatch from the shrimp fishery. These data were used by Gherard et al. (2013). In order to increase representation of size and age classes that were scarce in the dataset used by Gherard (2013), we collected 219 additional samples in 2012-2013 from the bycatch of other fisheries (e.g., shrimp), fishery-independent sampling of small individuals (<30 cm TL), and the commercial Gulf Corvina fishery. All fish were deceased at the time of collection from fishers. The research protocol was approved under UCSD IACUC ID no. S13240 and data were collected under CONANP permit no. CNANP-00-007.

Otolith preparation and ageing protocols were followed according to the methods developed by Gherard et al. (2013) for Gulf Corvina. Whole sagittal otoliths were first mounted on wood blocks with a cyanoacrylate adhesive and a 0.5 mm dorsal-ventral cross-section was cut through the otolith focus using a double-bladed Buehler Isomet 1000 precision saw (Allen et al.,

1995). Sub-sections were then mounted on a glass slide using thermoplastic glue and submerged in a glass petri dish with water and a black background. Transmitted light under a Zeiss Stemi 2000-C microscope with a Zeiss Axiocam 105 color camera at 6.25x total magnification was used to count the alternating opaque and translucent growth zones that define an annulus (Figure 2.1). For the purposes of this study, an annulus was defined as one full opaque and translucent zone of growth (Cailliet et al., 1996), which was validated for Gulf Corvina by previous studies (Rowell et al., 2005; Román-Rodriguez, 2000; Gherard et al., 2013) Each otolith was aged by two independent readers from digital images of cross-sections, as direct observation through the scope did not distort band pattern and did not affect age estimates. Samples were excluded from analysis when discrepancies between readers occurred.

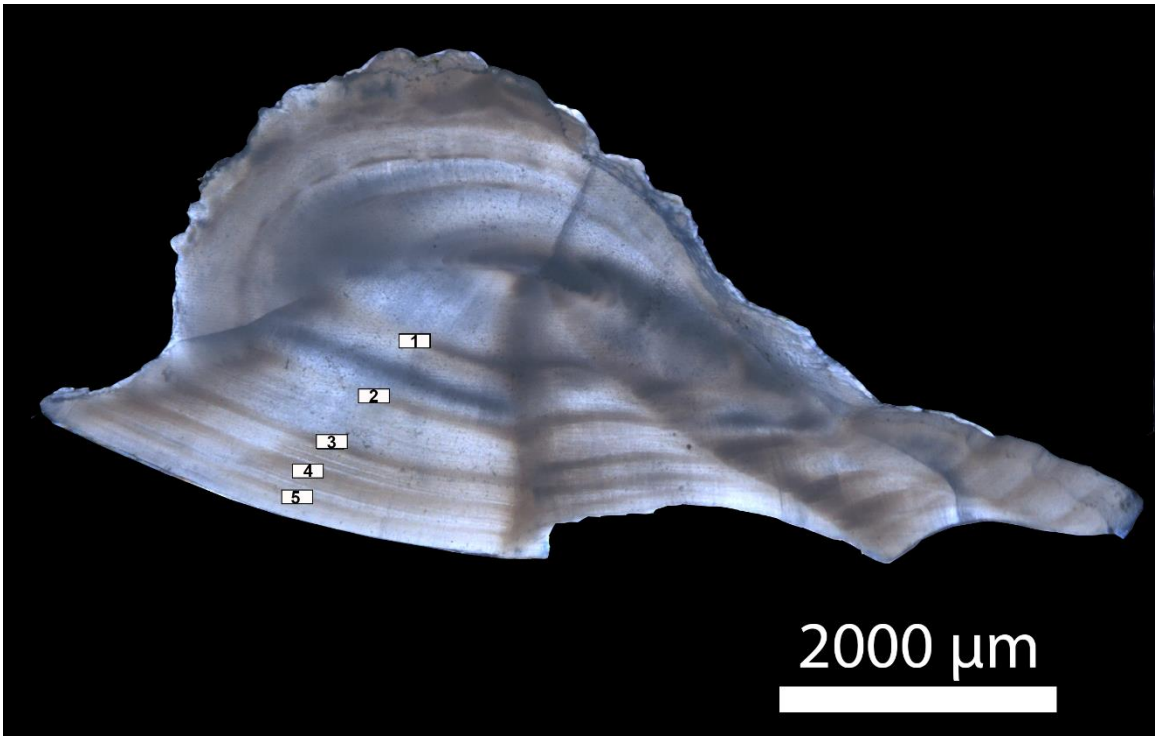

Figure 2.1: Transverse section of a sagittal otolith from a five-year old Gulf Corvina. Annuli are numbered and marked by white rectangles. Transmitted light under a Zeiss Stemi 2000-C microscope with a Zeiss Axiocam 105 color camera at 6.25 x total magnification was used to count the alternating opaque and translucent growth zones that define an annulus.

Model Fitting and Assessment of Fit

Growth modelling

A suite of growth models was fit to age data determined from otoliths as described, and length data obtained in the field. Model parameters were estimated using non-linear least squares regression with the Levenberg-Marquardt algorithm, and confidence limits were placed around parameter estimates in R studio (using the R packages FSA, minpack.lm, and nlstools).

The specialized von Bertalanffy growth model (von Bertalanffy, 1938) is given by:

Eq. 1: $$L(t) = L_{\infty}[1 - e^{-K(t-t_0)}]$$

where $L(t)$ is size (in mm TL) at age t, L_{∞} is the maximum average length (in mm TL), K is the growth rate coefficient (in year^{-1}), and t_0 is the theoretical age at which length is zero (in years).

The Gompertz growth model (Gompertz, 1825) is given by:

Eq. 2: $$L(t) = L_{\infty} e^{(-\left(\frac{1}{K}\right)e^{-K(t-t_0)})}$$

where the parameters are the same as described for Eq. 1.

The logistic model (Ricker, 1975) is given by:

Eq. 3: $$L(t) = L_{\infty}[1 + e^{-K(t-t_0)}]^{-1}$$

where the parameters are the same as described for Eqs. 1 and 2.

The Schnute model where a and b are not equal to zero (Schnute, 1981) is given by:

Eq. 4: $$L(t) = \left[{L_1}^b + ({L_2}^b - {L_1}^b)\frac{1-e^{-a(t-\mathrm{T}_1)}}{1-e^{-a(\mathrm{T}_2-\mathrm{T}_1)}}\right]^{1/b}$$

where T_1 is the first specified age, T_2 is the second specified age, L_1 is size at age T_1, L_2 is size at age T_2, a is the constant relative rate of relative growth (in year^{-1}), and b is the incremental relative rate of relative growth (dimensionless),

Finally, the Schnute-Richards model (Schnute and Richards, 1990) is given by:

Eq. 5: $$L(t) = L_{\infty}\left(1 + \alpha e^{-at^c}\right)^{1/b}$$

where $\alpha, b,$ and c are dimensionless parameters, and a has the unit of year^{-b}.

Statistical measures of fit

Model fit was assessed with the bias-corrected Akaike Information Criterion (AICc) (Shono, 2000; Burnham and Anderson, 2004), and Bayesian Information Criterion (Schwarz, 1978) in R Studio (using the R package AICcmodavg).

The formula for AICc is given by:

Eq. 6: $$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

where:

Eq. 7: $$AIC = -2\log(L) + 2k$$

and n is the number of observations, k is the number of model parameters, and L is the likelihood.

The formula for BIC is given by:

Eq. 8: $$BIC = 2\ln(L) + k\log(n)$$

where parameter definitions are the same as described for Eq. 7.

The smallest AICc and BIC values indicate the best model. The difference between the two criteria is that AICc is designed to select the model that describes reality the best while treating no models as true, which is consistent with an information theory approach, whereas BIC is designed to select the true model. Practically, BIC penalizes for the number of parameters more heavily than AICc. AICc was used instead of AIC as it is bias-corrected at small n values or high k:n ratios; AICc converges to AIC at large n values (Burnham and Anderson, 2004). AICc and BIC values were calculated to show the absolute difference between model fits. Next, AICc weights were calculated for model averaging of parameter estimates; the AIC weighting formula is given by:

Eq. 9: $$w_i = \frac{e(-0.5\Delta_i)}{\sum_{k=1}^{5} e(-0.5\Delta_k)}$$

where parameter definitions are the same as described for Eqs. 7 and 8.

Simple Indicators of Biased Data

Simulation of an ideal sampling outcome

To test for the influence of sampled population structure on growth model output, different amounts of simulated data were added to raw data so that each age observed (1-8) had 200 total

observations. Data were simulated from a normal distribution with the same mean and standard deviation as the raw data at each age class. This simulation was not intended to generate the true population structure of Gulf Corvina in the Gulf of California, but rather to generate an equal number of samples in each age and size class. This simulation did not explicitly account for selectivity or limits in sampling effort, but filled in gaps left by these factors and others that prevented more equal representation of each size and age class in the raw data. Models were fit to the new dataset and goodness of fit was assessed in the same manner as was described above.

Froese and Binohlan's empirical relationship

Froese and Binohlan's (2000) empirical relationship between the longest fish in the data set (L_{max}) and L_∞ was used to specifically test for the influence of the lack of large and old fish in the raw dataset, which is likely due to heavy exploitation. If large and old fish are insufficiently represented in the dataset, it stands to reason that the L_∞ predicted by this relationship will be greater than the modelled L_∞. This relationship is given by:

Eq. 10: $$logL_\infty = 0.044 + 0.9841 * \log(L_{max})$$

Literature review

A brief literature review of sciaenid growth modelling was conducted to assess how the results of this study compared with other studies on fishes closely related to the Gulf Corvina (e.g., other species in the genus *Cynoscion*). In conjunction with Froese and Binohlan's empirical relationship and the simple simulation of an ideal sampling scenario, this brief literature review was intended to check if the samples used in this study produced a biologically plausible growth pattern when growth was modelled.

Simulations with a Per-Recruit Model

To be able to discuss the implications of misrepresenting growth in Gulf Corvina, we ran simulations with a per-recruit model detailed in Appendix S1. In brief, this per-recruit model estimates the female spawning-stock-biomass-per-recruit (SSBR; a proxy of reproductive

capacity) and yield-per-recruit (YPR; exploitable biomass) of Gulf Corvina in relation to the annual exploitation rates of the old adults (≥ 5 year-old individuals) of the species (E_{OA}). In this per-recruit model, Gulf Corvina is assumed to grow according to one of five alternative growth models: (1) the von Bertalanffy model developed in Gherard et al. (2013), referred to as the "Gherard model"; (2) the von Bertalanffy model fit to raw data in the present study; (3) the von Bertalanffy model fit to raw data bolstered by simulation values in this study; (4) the Schnute-Richards model fit to raw data in the present study; and (5) the Schnute-Richards model fit to raw data bolstered by simulation values in this study. The current E_{OA} was estimated to be 0.825 year^{-1} (Appendix 1). We first ran simulations with the per-recruit model to determine the maximum value of the YPR of Gulf Corvina (YPR_{max}) and the natural SSBR of Gulf Corvina (NSSBR), i.e., its SSBR in the absence of fishing (Appendix 1). Then, we estimated the current fraction of NSSBR (current FNSSBR, i.e., the ratio of current SSBR to NSSBR) and the current YPR over YPR_{max} of Gulf Corvina, when each of the five abovementioned growth models is used to represent the growth in length of Gulf Corvina.

RESULTS

Length and Age Structure

A bimodal distribution was observed in the length and age structure of the fish used in this study (Figures 2.2 and 2.3). The first mode of the distribution represents Gulf Corvina caught as bycatch, whereas the second represents Gulf Corvina caught in the targeted fishery. Lengths ranged from 141-1013 mm TL, and ages ranged from 1-8 years.

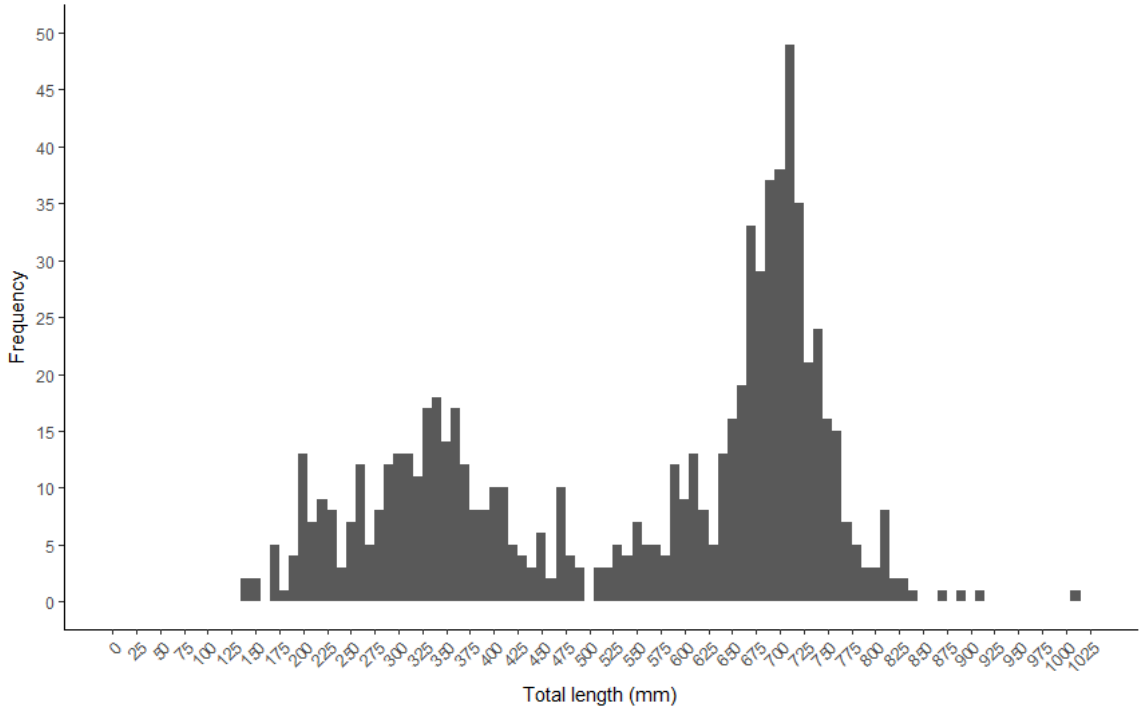

Figure 2.2: Total length frequency of Gulf Corvina from raw data represented in 10mm bins. A bimodal distribution was observed, with the first consisting of Gulf Corvina caught as bycatch, and the second largely consisting of fish from the directed fishery. Few fish larger than 750 mm are present in this dataset

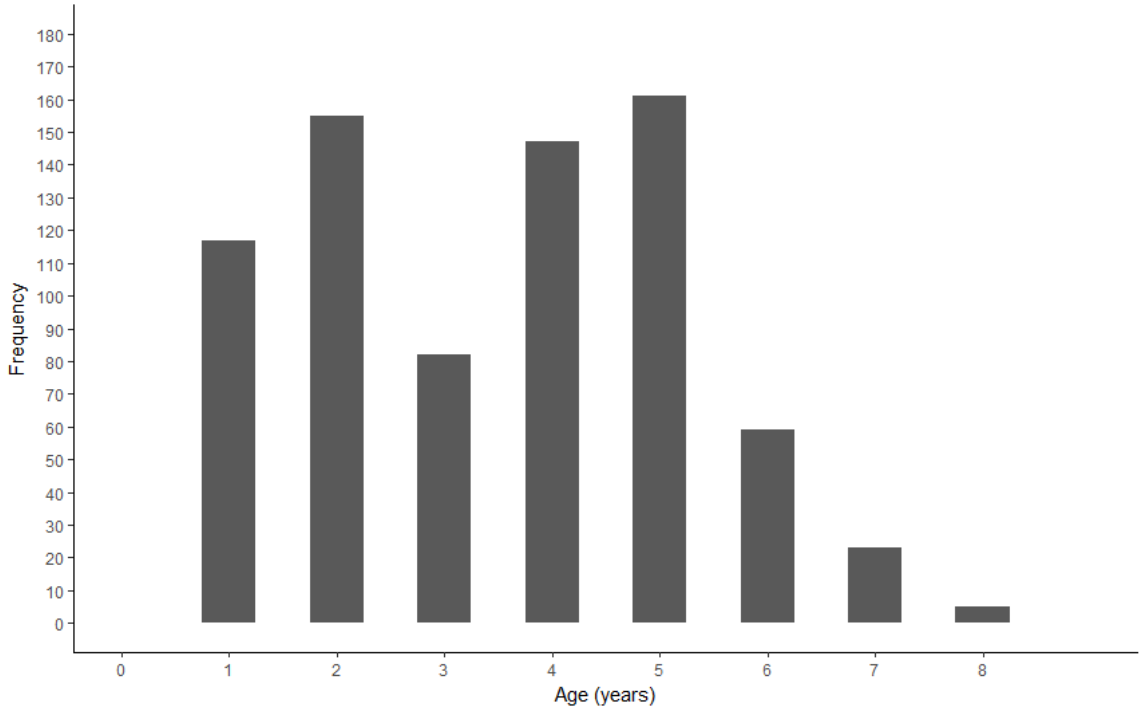

Figure 2.3: Age frequency of Gulf Corvina from raw data. A bimodal distribution was observed, with the first consisting of Gulf Corvina caught as bycatch, and the second largely consisting of fish from the directed fishery. Few fish older than age 6 are present in this dataset.

Model Fitting and Assessment of Fit for Models Fit to Raw Data

Growth patterns and parameter estimates for models fit to raw data

The Gompertz, logistic, and von Bertalanffy models yielded asymptotic growth patterns, while the Schnute-Richards model described biphasic growth and the Schnute model described near-linear growth after 1.5 years of life (Figure 2.4). Modelled length at age was most similar among models at intermediate ages, where samples were most abundant (Figure 2.4). Conversely, modelled length at age was most variable at young and old ages, where samples were most scarce (Figure 2.4). Estimates of L_∞ ranged from 730.91 mm (Schnute-Richards model) to 916.05 mm (von Bertalanffy model). All parameter estimates are summarized in Table 2.1, while confidence intervals around parameter estimates are reported in Appendix 1.

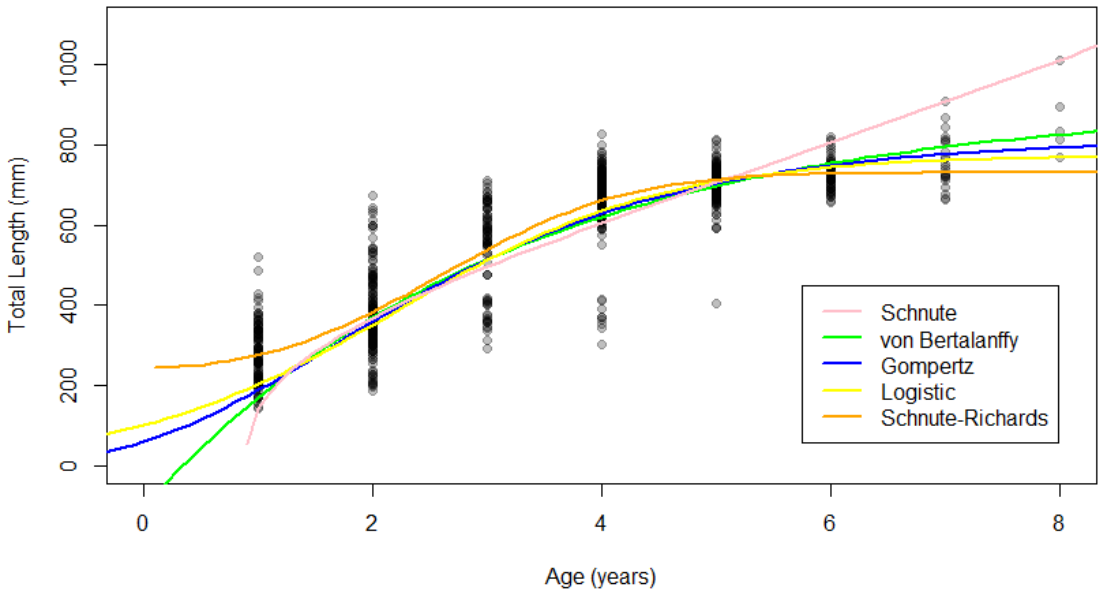

Figure 2.4: Growth models fit to raw age-length data for Gulf Corvina. The Gompertz, Logistic, and von Bertalanffy models yielded asymptotic growth patterns. However, the Schnute_Richards model described bi-phasic growth, and the Schnute model describes near-linear growth after the first 1.5 years of life. Differences in modelled size at age were most pronounced at the beginning and end of life, where samples were most scarce.

Table 2.1: Parameter estimates for growth models fit to raw age-length data for Gulf Corvina. Estimates of L_∞ were variable, but not as variable as those reported in previous multi-model studies of Gulf Corvina growth (Aragon-Noriega, 2014; Mendivil-Mendoza et al., 2017). Confidence intervals around parameter estimates may be found in the Supplemental Information.

Model name	Model equation when fit to raw data
von Bertalanffy	$L(t) = 916.05[1 - e^{-0.28(t-(-0.17))}]$
Gompertz	$L(t) = 820.64e^{(-(\frac{1}{0.51})e^{-0.51(t-1.29)})}$
Logistic	$L(t) = 778.88[1 + e^{-0.76(t-1.92)}]^{-1}$
Schnute	$L(t) = \left[141^{-0.33} + (1013^{-0.33} - 141^{-0.33})\frac{1 - e^{-3.36(t-1)}}{1 - e^{-3.36(8-1)}}\right]^{1/-0.33}$
Schnute-Richards	$L(t) = 730.91\left(1 + (-0.003)e^{-(0.12)t^{2.18}}\right)^{1/0.003}$

Measures of statistical fit for models fit to raw data

AICc and BIC values indicated that the Schnute-Richards model described the raw data best, followed by the logistic, Gompertz, von Bertalanffy, and Schnute models (Table 2.2). The AIC weighting formula gave full support to the Schnute-Richards model, so no model averaging of parameters was necessary.

Table 2.2: Statistical measures of fit for growth models fit to raw age-length data for Gulf Corvina. The Schnute-Richards model fit the data best according to AICc and BIC values, but is only marginally better than the logistic, Gompertz, and von Bertalanffy models. Note: K indicates the number of parameters. Note: *three parameters were estimated by nonlinear least squares, but four additional parameters were manually inputted (maximum and minimum ages and lengths) for the Schnute model.

Model	K	AICc	Δ AICc	AICc weight	BIC	Δ BIC
Schnute-Richards	6	8759.82	0.00	1	8787.42	0.00
Logistic	4	8773.62	13.80	0	8792.04	4.62
Gompertz	4	8789.69	29.87	0	8808.11	20.69
von Bertalanffy	4	8813.66	53.84	0	8832.08	44.66
Schnute	3*	9148.78	388.96	0	9162.61	375.19

Simple Indicators of Biased Data

Growth patterns and parameter estimates for models fit to raw data bolstered by simulated values

The Schnute-Richards, Gompertz, logistic and von Bertalanffy growth models yielded asymptotic growth patterns, while the Schnute model described near-linear growth after 1.5 years of age (Figure 2.5). Modelled length at age was similar at intermediate ages among all growth models except for the Schnute one, but differed slightly at young and old ages (Figure 2.5). Estimates of L_∞ ranged from 834.34 mm (logistic model) to 951.30 mm (von Bertalanffy model) (Table 2.3). All parameter estimates for each growth model are summarized in Table 2.3.

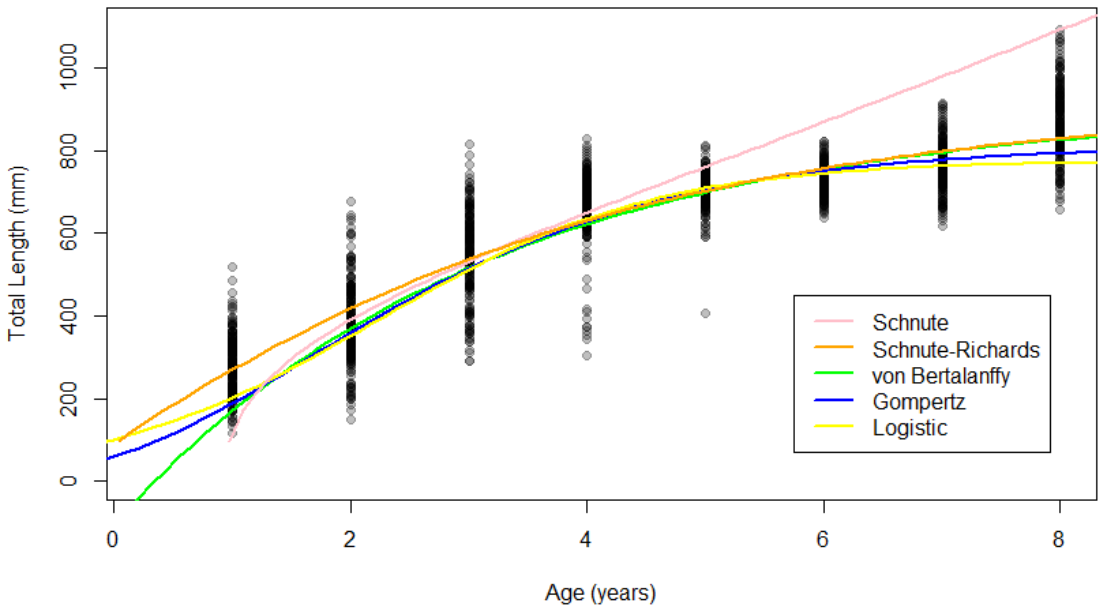

Figure 2.5: Growth models fit to raw Gulf Corvina age-length data bolstered by simulated values. All models except for the Schnute described asymptotic growth, and only showed slight differences in modelled size at age. Differences in modelled size at age were most pronounced at the beginning and end of life.

Table 2.3: Parameter estimates for growth models fit to raw Gulf Corvina age-length data bolstered by simulated values. Compared to parameter estimates for models fit to raw data alone, estimates of L_∞ were less variable and generally increased. These estimates are closer to the L1 of 1,006 predicted by Froese & Binohlan's (2000) empirical relationship between L_∞ and the longest fish in a dataset.

Model	Model fit to data bolstered by simulated values
von Bertalanffy	$L(t) = 951.30[1 - e^{-0.25(t-(-0.33))}]$
Gompertz	$L(t) = 870.48e^{(-(\frac{1}{0.62})e^{-0.62(t-1.34)})}$
Logistic	$L(t) = 834.34[1 + e^{-0.62(t-2.10)}]^{-1}$
Schnute	$L(t) = \left[141^{-0.78} + (1013^{-0.78} - 141^{-0.78})\frac{1 - e^{-6.06(t-1)}}{1 - e^{-6.06(8-1)}}\right]^{1/-0.78}$
Schnute-Richards	$L(t) = 938.80\left(1 + (-0.0046)e^{-(0.67)t^{0.72}}\right)^{1/0.0019}$

Measures of statistical fit for models fit to raw data bolstered by simulated values

The von Bertalanffy growth model described the raw data bolstered by simulated values best according to AICc and BIC values (Table 2.4). However, it was only marginally better than the Schnute-Richards and Gompertz models based on AICc. Thus, the von Bertalanffy growth model received 53% of AICc weighting to the Schnute-Richards' 33%, and Gompertz' 15%. The logistic model fit the data better than the Schnute model, but neither models received any support from AICc weighting. Model averaging L_∞ based on AICc weights resulted in an estimated L_∞ of 945 mm, an estimate 6 mm shorter than the that predicted by the von Bertalanffy model. In contrast to AICc values, BIC values indicated that the Gompertz model fit the data better than the Schnute-Richards model. Both Gompertz and Schnute-Richards models fit the data better than the logistic and Schnute models according to BIC values, as was indicated by AICc values.

Table 2.4: Statistical measures of fit for growth models fit to raw Gulf Corvina age-length data bolstered by simulated values. The von Bertalanffy growth model described the data best according to AICc and BIC values. However, AICc weighting indicated that the Schnute- Richards and Gompertz models had nearly equivalent fits. Note: K indicated the number of parameters in each model. Note: *three parameters were estimated by nonlinear least squares, but four additional parameters were manually inputted (maximum and minimum ages and lengths) for the Schnute model.

Model	K	AICc	Δ AICc	AICc weight	BIC	Δ BIC
von Bertalanffy	4	18678.72	0.00	0.53	18700.20	0.00
Schnute-Richards	6	18679.65	0.94	0.33	18711.87	11.67
Gompertz	4	18681.29	2.57	0.15	18702.77	2.57
Logistic	4	18702.60	23.89	0	18724.09	23.89
Schnute	3*	19891.72	1213.01	0	19907.84	1207.64

Froese and Binohlan's empirical relationship

Froese and Binohlan's empirical relationship between L_{max} and L_∞ predicted a L_∞ of 1006 mm from a maximum observed length of 1013 mm. This estimate is larger than all estimates of L_∞ derived from growth models fit to raw data (Table 2.1) and raw data bolstered by simulated values (Table 2.3).

Literature review

Results from our review of 24 sciaenid growth studies and citations are summarized in Table 2.5. Age and body length relationships in sciaenids were represented by the von Bertalanffy growth model in 20 of 24 (83%) of the studies we reviewed, as reported in Atlantic Croaker (*Micropogonias undulatus*), Black Drum (*Pogonias chromis*), Red Drum (*Scianops ocellatus*), Southern Kingfish (*Menticirrhus americanus*), Spotted Seatrout (*Cynoscion nebulosus*), Weakfish (*Cynoscion regalis*), and Whitemouth Croaker (*Micropogonias furnieri*). Notably, growth of the Totoaba (*Totoaba macdonaldi*), a sciaenid closely related to Gulf Corvina and also found in the

Gulf of California, was modelled by the von Bertalanffy growth model. Growth of the Gulf Corvina was modelled using the von Bertalanffy growth model in two previous studies.

Other growth models have been used to describe age and body length relationships in sciaenids in 5 of 24 (21%) the studies we reviewed. The Gompertz model was used to model growth in female Spotted Seatrout. A linear model was used to model growth in male Spotted Seatrout, although it was noted that the linear growth pattern may have been due to lack of sampling of large and old individuals. Multi-model approaches similar to this study were employed three times (13%). One study on the Gulf Corvina selected the von Bertalanffy growth model for two datasets, and the Schnute-Richards model for two other datasets. As such, this study was counted in as one of the 20 studies that used the von Bertalanffy growth model to model sciaenid growth, and as one of the five studies that employed other growth models. The most recent age and growth study on Gulf Corvina selected the Schnute-Richards model, but did not describe a biphasic growth pattern. The other study that employed multiple models fit them to Spotted Seatrout age-length data and found the most statistical support for the three-parameter logistic model.

Table 2.5: Models used to describe growth in sciaenid fishes similar to and including the Gulf Corvina. A review of 24 sciaenid growth studies indicated that sciaenid growth is most commonly modelled by the von Bertalanffy growth model (20 studies; 83% of studies reviewed).

Growth model selected	Genus and species	References
Gompertz	*Cynoscion nebulosus*	Murphy and Taylor, 1994 (females only)
Linear	*Cynoscion nebulosus*	Murphy and Taylor, 1994 (males only); Nieland et al., 2001
Logistic	*Cynoscion nebulosus*	Dippold et al., 2016
Schnute-Richards	*Cynoscion othonopterus*	Aragón-Noriega, 2014 (selected for two datasets); Mendivil-Mendoza, 2017
von Bertalanffy	*Cynoscion nebulosus*	Rutherford et al., 1982; Maceina et al., 1987; Wieting, 1989; Cottrell, 1990
	Cynoscion othonopterus	Gherard et al. 2013; Aragón-Noriega, 2014 (selected for two datasets)
	Cynoscion regalis	Lowerre-Barbieri et al., 1995; Hatch and Jiao, 2016; White, 2017
	Menticirrhus americanus	Clardy et al., 2014
	Micropogonias funieri	Manickchand-Heileman and Kenny, 1990; Santos et al., 2017
	Micropogonias undulates	Barger, 1985; Barbieri, 1993; Franco, 2014
	Pogonias chromis	Murphy and Taylor, 1989
	Sciaenops ocellatus	Beckman et al., 1988; Murphy and Taylor, 1990; Ross et al., 1995
	Totoaba macdonaldi	Rodriguez and Hammann, 1997

Model Selection

Synthesis of the above considerations and assessments led to the selection of the von Bertalanffy growth model as the best model to represent Gulf Corvina growth. Of models fit in this study, the von Bertalanffy growth model had the 4th best statistical fit to raw data (AICc = 8813.66, Δ AICc = 53.84, AICc weight = 0; BIC = 8832.08, Δ BIC = 44.66; Table 2.2) and the best statistical fit to raw data bolstered by simulated values (AICc = 18678.72, Δ AICc = 0. AICc

weight = 0.53; BIC = 18700.20, Δ BIC = 0; Table 2.4). Of models fit in this study, the von Bertalanffy growth model produced an L_∞ closest to the L_∞ predicted by Froese and Binohlan's empirical relationship of 1006 mm (raw data: 916.05 mm; raw data bolstered by simulated values: 951.30 mm; Tables 1 and 3). Further, the von Bertalanffy growth model was used to represent sciaenid growth in 83% of studies reviewed.

Simulations with a Per-Recruit Model

The current value of the exploitation rate of old adults of Gulf Corvina E_{OA} that we estimated is *ca.* twice larger than the value of E_{OA} at which the YPR of Gulf Corvina reaches a maximum, regardless of the growth model employed for simulations with the per-recruit model (Appendix S1). However, the current FNSSBR of Gulf Corvina predicted when using the Schnute-Richards growth model fit to raw data only (0.60) is noticeably greater than the current FNSSBR of Gulf Corvina predicted when using all the other growth models (0.42-0.53) (Figure 2.6A). The value of fraction of natural SSBR that causes population collapse typically is in the range of 0.1-0.6 and lower for short-lived fish species such as Gulf Corvina (Myers et al., 1999; Grüss et al., 2014). Thus, the per-recruit model employing Schnute-Richards growth model predicts the Gulf Corvina stock to be in a much healthier state than the per-recruit models employing other growth models. The current YPR over YPR_{max} of Gulf Corvina predicted when using the Schnute-Richards growth model fit to raw data only (0.80) is also greater than the current YPR over YPR_{max} of Gulf Corvina predicted when using all the other growth models (0.70-0.74) (Figure 2.6B).

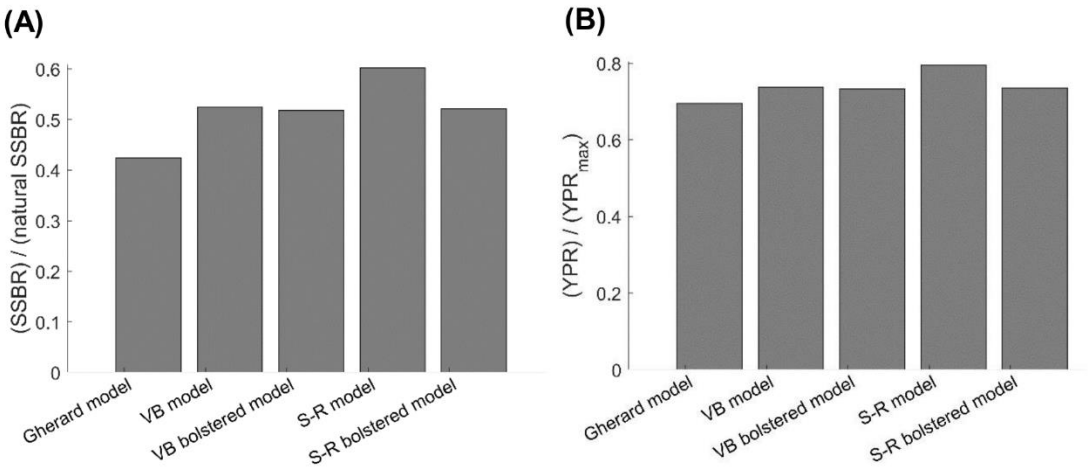

Figure 2.6: Consequences of using different growth models on (A) the current female SSBR over natural SSBR and (B) current YPR over YPR_{max} of Gulf Corvina (*Cynoscion othonopterus*). Per-recruit models employing the S-R growth model showed the stock to be in a healthier state than per-recruit models employing other growth models. SSBR, spawning-stock-biomass-per-recruit; YPR, yield-per-recruit; Gherard model, von Bertalanffy model developed in Gherard et al. (2013); VB model, von Bertalanffy model fit to raw data in the present study; VB bolstered model, von Bertalanffy model fit to raw data bolstered by simulation values in this study; S-R model, Schnute_Richards model fit to raw data in the present study; S-R bolstered model, Schnute_Richards model fit to raw data bolstered by simulation values in this study.

DISCUSSION

This study illustrates the pitfalls of using statistical considerations alone when selecting a growth model for a vulnerable and highly-exploited species, due to the high likelihood of a biased distribution of samples. The combination of highly efficient, size-selective gear and high fishing effort have altered the age structure of the Gulf Corvina population (Ortiz et al., 2016), making sufficient representation of each size and age class difficult (Erisman et al., 2014). The influence of the lack of large and old fish in the dataset used for this study is clear, as Froese and Binohlan's (2000) empirical relationship predicted an L_∞ that was 89.95 – 275.09 mm greater than the L_∞ predicted by growth modeled fit to raw data. This predicted L_∞ from Froese and Binohlan's (2000) empirical relationship of 1006 mm was identical to the L_∞ estimated by Gherard et al. (2013) with

the von Bertalanffy growth model. Growth patterns (Figures 4 and 5) and parameter estimates (Tables 1 and 3) were far less variable for models fit to data where sample size was equal at age, compared to models fit to raw data alone.

Unfortunately, heavy exploitation of Gulf Corvina makes the use of biased data in age and growth studies an unavoidable reality. Length data collected from the continuous monitoring of the fishery (Erisman et al., 2015; Ortiz et al., 2016) indicate that Gulf Corvina may be able to grow longer than their maximum reported length of 1013 mm and live longer than their maximum reported age of 9 years, but heavy exploitation (exploitation rate of 0.825 $year^{-1}$ for Gulf Corvina five years-old and older; Erisman et al. 2014) prevents them from doing so. Thus, despite our best efforts, we were unable to sufficiently represent large and old fish in our dataset. Further, while we made a concerted effort to sample small individuals, our data set would have been improved if we were able to collect more. This led to our decision to employ our simulation exercise to understand how the biases in our data affected our results. Similarly biased data have been the only data available for age and growth studies with Gulf Corvina, and previous studies have taken markedly different approaches to dealing with its limitations. Gherard et al. (2013) chose to use the inflexible and widely comparable von Bertalanffy growth model while acknowledging the data's limitations and caveating results accordingly. Alternatively, Aragón-Noriega (2014) and Mendivil-Mendoza (2017) employed a multi-model approach that leaned exclusively on statistics. Their statistical procedures led to the selection of the flexible Schnute-Richards model to describe Gulf Corvina growth. Despite reporting different growth patterns depending on which dataset was used, Aragón-Noriega (2014) did not acknowledge the limitations of fishery-dependent data and concluded that Gulf Corvina grew in a biphasic pattern.

The same suite of models employed by Aragón-Noriega (2014) and Mendivil-Mendoza et al. (2017) were fit to our data, and statistical measures of fit similarly supported the Schnute-Richards model as the best model for Gulf Corvina. Further, a biphasic growth pattern was described by the model, as it did in Aragón-Noriega's (2014) study. However, our review of 24 sciaenid growth studies indicated that only two (8%) studies used the Schnute-Richards model to

describe sciaenid growth (Aragon-Noriega, 2014; Mendivil-Mendoza et al., 2017), of which only one described biphasic growth (Aragón-Noriega, 2014). The biological implausibility of this growth pattern was further supported by the distance between Froese and Binohlan's predicted L_∞ and the L_∞ estimated by the Schnute-Richards model (1006 vs. 730.91 mm, i.e., a 275.09 mm difference). Finally, simulating an ideal sampling scenario where each age class was equally represented revealed that this biphasic growth pattern was due to bimodal distribution of samples and a lack of large, old fish. Both the parameter estimates and growth pattern changed substantially when simulated data was added to raw data so that sample size was equal for each age (Figure 2.5 and Table 2.3). The Schnute-Richards model is flexible by design, and is, therefore, not suited for use with datasets that do not sufficiently represent each size and age class. Thus, by integrating the results of our statistical measures of fit, literature review, and simple indicators of biased data, we selected the von Bertalanffy growth model as the best model to represent Gulf Corvina growth.

The results of our study reinforce the well-established, but often forgotten, principle that each size and age class must be sufficiently represented for growth modelling to produce biologically reasonable results (Cailliet et al., 1986; Cailliet and Tanaka, 1990; Francis and Francis, 1992; Cailliet and Goldman, 2004). Ensuring sufficient representation may be difficult for highly-exploited fishes, as exploitation alters the population structure of fishes by preferentially selecting for large and old fish individuals (Berkeley et al., 2004; Mason, 1998). Similar challenges are faced when studying growth for vulnerable fishes or in data-poor fisheries, where there may not be resources available for extensive fishery-independent sampling or fish are scarce in general. Despite difficulty, ensuring sufficient representation of each size and age class should be a priority. The distinction between sampling to sufficiently represent each size and age class and sampling to represent population structure is an important one to make, as sampling to represent population structure should not be a goal of age and growth studies due to the bias created by the natural scarcity of large and old fish. As such, the simple simulation of an ideal sampling scenario with an equal number of samples at each age was not intended to represent the population structure of Gulf

Corvina or to reflect the relative probability of obtaining samples of particular size and age classes in the real world.

Life-history parameters such as those estimated in growth models are influential in assessments for vulnerable and data-poor species (Fournier et al., 1990; Dulvy et al., 2004; Froese, 2004; Honey et al., 2010; Hordyk et al., 2016). These types of assessments rely on age-length data to determine vulnerability and overfishing, and problems emerge when all size and age classes are not sufficiently represented. The average maximum length (L_∞) is underestimated and the growth rate (K) is overestimated when large and old fish are absent. Accordingly, a short generation time and lower levels of mortality are estimated, conferring more resilience to exploitation that the population possesses (Campana, 2001; Goldman et al., 2012; Harry, 2017). This idea was demonstrated with simulations with a per-recruit model, where the per recruit model using the Schnute-Richards growth model fit to raw data (which had the lowest L_∞ in the present study) predicted Gulf Corvina reproductive capacity to be in a much healthier state than the per recruit models using other growth models (Fig. 2.6A). This false resiliency makes fishery management measures less effective (Campana, 2001; Cailliet and Andrews, 2008; Goldman et al., 2012), and may be present in Gulf Corvina assessments, as length and age truncation in the catch has increased progressively since biological monitoring of the fishery began in 1997 (Erisman et al., 2014). Given this length and age truncation, published growth models reported for this species may not be representing biology but rather the influence of exploitation.

Our results have implications for estimating growth within a stock assessment. Piner (2016) documented an increase in precision in parameter estimates, ability to account for selectivity, and ability to incorporate multiple data sources when growth was estimated within a stock assessment. However, the influence of sample distribution on model output should be carefully examined if this approach is to be taken. So-called haphazard sampling strategies that ensure that all age and size classes are represented (e.g. Wells et al., 2013) make growth estimation within a stock assessment model more difficult, though are necessary if the density of samples at a particular age

is driving model fit or preventing accurate estimation of L_∞. Precision may be improved, but care must be taken to ensure that precision is being improved around biological reality.

We found that Gulf Corvina exhibit a high degree of variation in length-at-age, a pattern that is common among coastal fishes in the Gulf of California and other regions of the eastern Pacific characterized by significant annual variations in precipitation, ocean temperatures, and productivity in response to climate forcing that are known to influence growth rates in marine fishes (e.g., El Niño Southern Oscillation, ENSO; (Wells et al., 2006; Williams et al., 2007; Black, 2009). Specifically, growth rate is higher in Gulf Corvina during El Niño years, mainly in association with increased sea surface temperatures in the region (Reed, 2017). ENSO has been shown to affect fish growth in other areas, such as the waters of New Caledonia (Lehodey and Grandperrin, 1996), New Zealand (Gillanders et al., 2012), and north-western Australia (Ong et al., 2016, 2015). As the present study was conducted over multiple years, it is reasonable to assume that variations in ENSO over the study period (i.e., a succession of El Niño/La Niña events) could have affected the fish harvested for this study, explaining the observed variation in length-at-age. These effects may affect estimates of growth derived with growth models, but in order to identify these effects with confidence, complete sampling must be conducted with this purpose in mind. Another explanation for length-at-age variation could be measurement error (Neilson, 1992; Campana, 2001). Most of the fish in this study were harvested during their spawning season, which is around the time when they form new annuli. Therefore, it would be reasonable to conservatively assume that the precision of this study is more or less one year of age. However, we have high confidence in our reading of these otoliths, as annuli are clearly seen with minimal preparation (Figure 2.1) and we excluded any samples for which there was a disagreement between readers.

Assessing the biological feasibility of growth model output, here accomplished with the use of simple indicators of biased data and literature review, is crucial for age and growth studies. Statistical measures of fit alone may not lead to the selection of a model that represents biological reality (Wang et al., 1995; Cailliet et al., 2006; Araya and Cubillos, 2006). By integrating measures of statistical fit with results from the simple indicators and literature review, we concluded that the

von Bertalanffy growth model best described the growth of Gulf Corvina and was most appropriate for the quality of available data. Though the Schnute-Richards model had the best statistical fit, it was not biologically reasonable, comparable between studies, or robust to biased data. Simple indicators such as those described in this paper should be used to reveal biases in data, and the use of flexible growth models such as the Schnute-Richards model to represent the growth of Gulf Corvina and similarly exploited fishes should be halted if biases are not accounted for.

CONCLUSIONS

Sample distribution influences growth model output, especially for flexible, statistically-driven models. Data used in growth modelling studies should be thoroughly examined for bias, as statistical measures of fit are insufficient for selecting a model that reflects biological reality. Reflecting biological reality in growth models is critical for vulnerable fish and in data-poor fisheries, where age-length data are integral to assessing vulnerability and overfishing. In this case, the von Bertalanffy growth model represented biological reality best among the models tested. We warn against the production and use of growth models without recognizing biases in data given the serious implications for stock assessments and the management of vulnerable fish populations and data-poor fisheries.

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Chapter 3: Environmental and structural drivers of fish distributions among petroleum platforms across the U.S. Gulf of Mexico[2]

ABSTRACT

Petroleum platforms in the U.S. Gulf of Mexico (GOM) are important habitats for fishes and support regional fisheries. However, drivers of the horizontal (i.e. latitudinal and longitudinal) and vertical (i.e. position in the water column) distribution patterns of fishes associated with these artificial habitats are not fully understood on a GOM-wide scale. To build upon previous studies on a large spatial scale and focus on species-specific drivers, we conducted 114 submersible-rotating drop-camera and water quality sonde surveys at 54 platforms throughout the GOM. We then fitted two sets of binomial generalized additive mixed models (GAMMs) integrating environmental and structural (i.e. characteristics of platforms) predictors to encounter/non-encounter data for 17 fish species, so as to understand their horizontal and vertical distribution patterns throughout the GOM in platform habitat. Significant predictors for horizontal distribution included distance from shore (Bermuda Chub *Kyphosus sectatrix*, Greater Amberjack *Seriola dumerili*, Vermilion Snapper *Rhomboplites aurorubens*), salinity (Bermuda Chub, Red Snapper *Lutjanus campechanus*), the number of platforms within five kilometers (Blue Runner *Caranx crysos*, Crevalle Jack *Caranx hippos*), and dissolved oxygen concentration (Red Snapper). Significant predictors for vertical distribution included temperature (Atlantic Spadefish *Chaetodipterus faber*, Bermuda Chub, Blue Runner, Greater Amberjack, Red Snapper), salinity (Greater Amberjack, Red Snapper), dissolved oxygen concentration (Red Snapper), and seafloor depth (Red Snapper). However, the majority of the study species were not influenced by the predictors included in the horizontal (11/17 species) and vertical distribution (12/17 species)

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GAMMs. Thus, many GOM fishes were found to associate with platforms over a relatively wide range of environmental conditions and platform characteristics. This suggests specific environmental conditions and distinct platform characteristics may not be as important as the simple number of available platforms for determining the distributions of many platform-associated fishes in the GOM.

INTRODUCTION

Human activities have provided a vast amount of artificial reef habitat in the U.S. Gulf of Mexico (hereafter simply referred to as 'GOM') (Scarborough Bull and Kendall 1994; Stanley and Wilson 1996). In particular, oil and gas extraction has necessitated the construction of over 4,500 structures (including platforms and wellheads and excluding caissons, hereafter simply referred to as 'platforms') throughout the history of the GOM, many of which are found in mud bottom areas devoid of similarly complex, high-relief habitat (Gallaway and Cole 1998, BOEM 2019). At present, more than 1,400 standing petroleum platforms of the GOM provide important habitat for many species targeted by fisheries for at least part of their life cycle (e.g. Red Snapper *Lutjanus campechanus*; reviewed in Gallaway et al. 2009). Association with structures such as petroleum platforms may increase encounter rate with conspecifics and prey, provide a balance of resting and foraging habitat, and increase settlement opportunities for fish larvae (Fréon and Dagorn 2000; Hernández-Arana et al. 2003; Genin 2004). As such, petroleum platforms influence the horizontal and vertical distributions of GOM reef-associated fishes, and are host to diverse communities of fishes, making them very popular targets for fishers (Gallaway and Lewbel 1982; Stanley and Wilson 2000; Cowan and Rose 2016).

Petroleum platforms are distributed throughout the GOM from Alabama to Texas, exposing platform-associated fishes to a relatively wide range of abiotic environmental conditions (henceforth 'environmental conditions') and providing ample opportunity for variation in species-specific horizontal and vertical distribution patterns. Much of the variation in environmental conditions in the GOM is due to Mississippi River discharge, which affects the nutrient loading,

primary productivity, dissolved oxygen (DO) concentration and salinity of surrounding waters (Rabalais et al. 2002a; Alexander et al. 2007). Boom-and-bust cycles in plankton populations in response to Mississippi-derived nutrients result in hypoxic 'dead zones' that occur in waters offshore of Louisiana and eastern Texas (Rabalais et al. 2002b). The influence of these zones is far-reaching, as the threshold for waters to be considered hypoxic (2 mg/L) is actually below the sublethal effect and lethal thresholds for some species (Vaquer-Sunyer and Duarte 2008). Adverse effects of low DO concentration may be exacerbated by other stressors, such as temperature (Nilsson et al., 2010), which may affect large-scale fish distributions via its effect on oxygen delivery to tissues (Pörtner 2001, 2010; Perry 2005, Pauly 2010, but see Jutfelt et al., 2018 and references therein). Further, in cases of thermal stress, differences in thermal tolerance among species influence the nature and timing of their interactions (Pörtner and Farrell 2008), which may ultimately affect their horizontal and vertical distributions.

Platform characteristics (e.g. number of legs, age, number of surrounding platforms, and length of the surrounding pipeline; hereafter also referred to as 'structural parameters') also vary considerably throughout the GOM. The complexity of reef structures has been shown to influence the settlement, abundance and biodiversity patterns of fish communities (Connell and Jones 1991; Almany 2004; Lingo and Szedlmayer 2006), and the age of the platform may contribute to how much it reflects the community found on nearby natural reefs (Perkol-Finkel et al. 2006). The density of other reefs also affects fish populations and communities, with high biomass and abundance of fishes typically associated with artificial reefs in areas with intermediate to low densities of other reefs (artificial reefs being non-platform in nature in the cited studies; Strelcheck et al. 2005; Froehlich and Kline 2015). Resident species associate with platforms either for cover alone (e.g. Atlantic Spadefish *Chaetodipterus faber*, Red Snapper) or for both food and cover (e.g. Gray Triggerfish *Balistes capriscus*, Greater Amberjack *Seriola dumerili*) (Gallaway 1981). Thus, regardless of what drives species to associate with platforms, the variability in platform characteristics across the GOM suggests that all platforms may not be of equal utility to fishes.

Prior work has defined five longitudinal provinces of faunal assemblages in the GOM (Pulley 1952; Gallaway 1981). One can, therefore, reasonably suspect that the distribution of platform-associated fishes will vary independently of the age and complexity of the platforms. The distribution of fish larvae and the location of frontal zones have an influence on the distribution and abundance of post-larval fishes, and likely contribute to this pattern (Govoni et al. 1989; Grimes and Finucane 1991; Cowen and Sponaugle 2009). Further adding to the potential for spatial variability, fishing effort is generally lower in areas that are long distances from ports (Sampson 1992; Caddy and Carocci 1999; McCluskey and Lewison 2008). Therefore, one may expect that fishing's negative effects on biodiversity and abundance (Pauly et al. 2002) may be lessened at platforms that are long distances away from shore in the GOM.

The substantial variation in environmental and structural parameters that fishes are exposed to on platforms, and their importance to valuable fisheries, have led to considerable effort to study fish assemblages on petroleum platforms in the GOM over the past decades. Gallaway and Lewbell (1982) defined three depth-based faunal assemblage zones for platforms in the GOM: the 'coastal' (shoreline – 30 m), 'offshore' (30 – 60 m), and 'bluewater' (> 60 m) zones. It has been suggested that fish assemblage is relatively consistent within each of the three depth zones, except for the identity of the most abundant 'keystone' species, which is typically a small pelagic fish (e.g. Blue Runner *Caranx crysos* or Atlantic Spadefish) (Stanley and Wilson 2003). However, fish assemblage on petroleum platforms has also been shown to be influenced by environmental conditions. These include the distribution of turbid water layers, temperature, salinity, DO concentration, primary productivity in the water column, and the extent to which platforms are exposed to Caribbean water masses (Gallaway and Lewbel 1982; Stanley and Wilson 1996, 1997, 2000, 2003; Munnelly et al. 2019). Further, the vertical distribution of fishes on platforms has been shown to be influenced by DO concentration (Stanley and Wilson 2004; Reeves et al. 2018; Munnelly et al. 2019) and artificial light (Barker et al. 2018).

Although several studies described variations in fish assemblages on petroleum platforms in the GOM, there was an opportunity to build upon their conclusions at a larger spatial scale to

better understand the drivers of species-specific horizontal (i.e. latitudinal and longitudinal on a large spatial scale) and vertical (position in the water column on a small scale) distribution patterns around platforms. To do this, statistical techniques capable of incorporating non-linear relationships and multiple predictors must be employed. Generalized additive models and their mixed-effects extensions, generalized additive mixed models (GAMMs), have been frequently used for understanding fish distributions in the GOM (e.g. Hazen et al. 2009; Rooker et al. 2012, 2013; Grüss et al. 2014; Hazen et al. 2016; Dance and Rooker 2019). GAMMs were employed in the present study because of this precedent, and due to the potential for non-linear relationships between environmental and structural parameters and fish probability of encounter (Grüss et al. 2018a). Sex ratios, growth rates, and other characteristics of fish populations that affect their productivity can vary across a species' biogeographic range (Conover and Present 1990; Adams et al. 2000; Liu et al. 2016). This may be the case for some platform-associated species; most notably for Red Snapper (*Lutjanus campechanus*), which is thought to be divided into eastern and western subpopulations that exhibit differences in population dynamics and morphometrics (Fischer et al. 2004; Liu et al. 2016; SEDAR 2018). This spatial variation, and the existence of strong differences in habitat availability and fishing effort across most marine regions, have led to a push for spatial assessments to be used as the basis for fishery management advice (Berger et al. 2017; Goethel and Berger 2017). Identifying the parameters responsible for shaping the distributions of species will aid in prioritizing sampling effort to address spatial data gaps, predicting future distribution shifts, understanding disaster impacts (e.g. oil spills), and setting the scale at which stock assessments (both spatially-explicit and conventional) and management are conducted. This knowledge can reduce uncertainty in assessments, helping managers make the decisions necessary to sustain productive fisheries and monitor ecosystem function in the face of changing climate and habitat availability. As such, the objective of this study was to identify the environmental and structural parameters having an influence on the horizontal and vertical distributions of conspicuous fishes associated with offshore petroleum platforms in the GOM.

METHODS

Study Area and Platform Selection

This study focused on 54 petroleum platforms in the GOM over a period of 2 years (May through August of 2017 and 2018). A stratified random sampling procedure among depth strata ('coastal': 10-30 m depth; 'offshore/bluewater': 31-75 m depth; and 'shelf margin': 76 – 150 m; *sensu* Gallaway and Lewbell 1982) was used to select platforms. The platforms selected over the 2 years of the study were distributed from 28.0573°N to 29.9259°N latitude and from -95.5651°E to -88.1583°E longitude (Fig. 3.1).

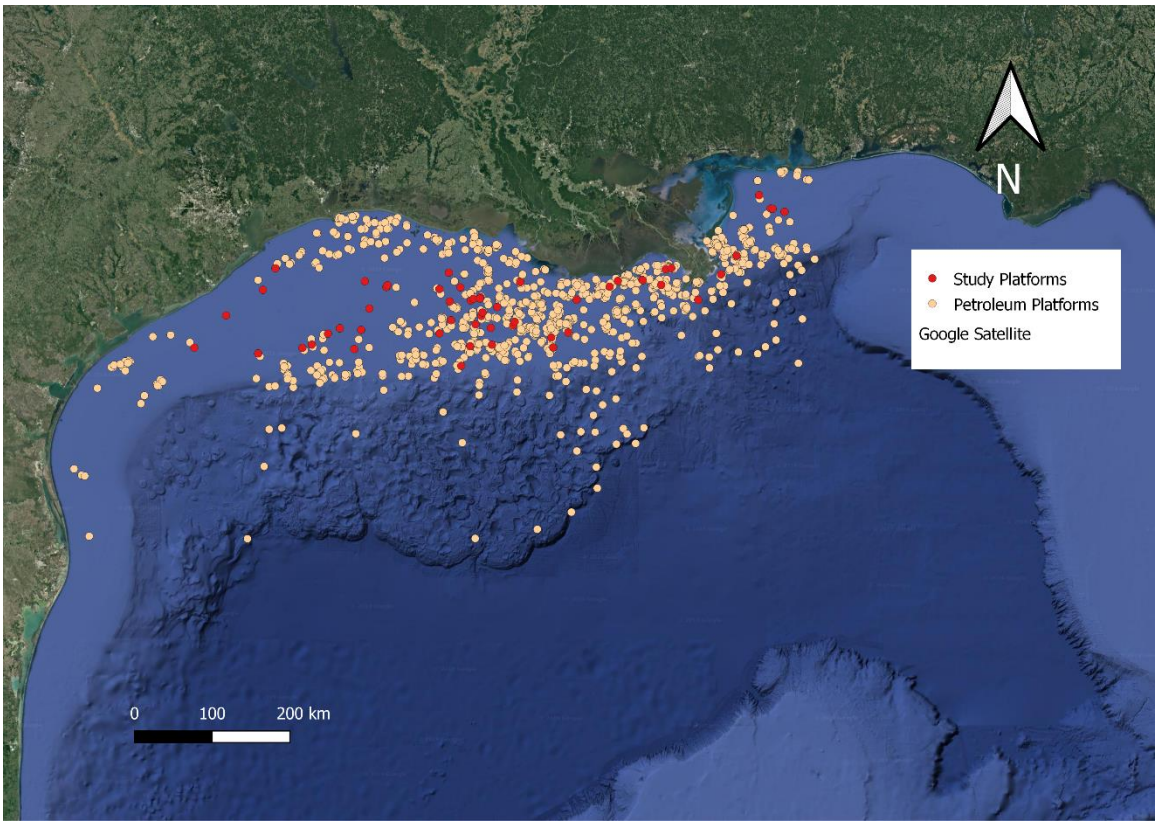

Figure 3.1: Distribution of platforms considered in this study (in red) in relation to the other petroleum platforms in the U.S. Gulf of Mexico.

Data Collection

Submersible-rotating video (SRV) camera and YSI EXO sonde surveys were conducted at the 54 study platforms by two survey teams in May – August of 2017 and 2018. Of the 54 study platforms, three were surveyed four times (twice in each year) and 51 were surveyed twice (in a single year). It was assumed that all study platforms were actively producing oil and gas at the time of the study. Of the 54 petroleum platforms studied, 18 were manned and 36 were unmanned. Whether a platform was manned or unmanned was not considered in our analyses, however, due to our observations of considerable activity on reportedly "unmanned" platforms (e.g. frequent visits by crew boats). Hurricanes Harvey and Irma both formed in late-August, 2017, but sampling was completed prior to their impact on the study area. SRVs were deployed on the down-current side of the platform for 6-7 min at each 10-m depth interval (hereafter referred to as 'standard drops'), and at one additional location within 100 m of the study platform in the same manner if a large school of fish was observed on a Simrad EK-80 echosounder (hereafter referred to as 'targeted drops'), which was to be used in a forthcoming complementary study. In parallel, a YSI EXO water quality sonde was deployed using bandit commercial fishing gear and allowed to reach the seabed, after which it was immediately retrieved. When depth prohibited the sonde from reaching the seabed, the sonde was lowered beyond the deepest SRV depth. The environmental parameters recorded by the sonde were DO concentration (mg/L), temperature (°C), and salinity (psu). These parameters were averaged across the entire water column for each combination of platform, survey team, and sampling date in a dataset later used to understand the parameters that affect fish horizontal distribution patterns (referred to as the 'horizontal distribution dataset'). In a second dataset employed to understand parameters affecting fish vertical distribution patterns (referred to as the 'vertical distribution dataset'), DO concentration, temperature and salinity were averaged within each 10-meter depth layers for each combination of platform, survey team, and sampling date. The sonde was calibrated prior to each survey event following the manufacturer's guidelines.

As it was not possible to quantitatively measure visibility at each 10-m depth interval, visibility was scored 1 – 3 by an analyst based on their ability to identify fishes at different distances away from the camera. This analysis was inherently qualitative because of the lack of direct visibility data and measurements of distance from the camera and fish sizes, but it was still possible to qualitatively discern if members of the same species occurred at multiple distances away from the camera. If fishes were only identifiable at one distance from the camera (i.e. all members of the same species exhibiting the same life stage morphology appeared at the same size on the screen), and if there was no structure observed in the distance, then the visibility score was a 1. If fishes were identifiable at two-to-three different distances from the camera (i.e. members of the same species exhibiting the same life stage morphology appeared at two-to-three different sizes on the screen, representing different distances away from the camera), or if the opposite side of the structure was visible in the distance, then the visibility score was a 2. Finally, if fishes were identifiable at more than three different distances from the camera (same criteria as 2, but with additional disparities in size on the screen), then the visibility score was a 3. In instances where the visibility score differed between the standard and targeted drops at the same depth interval, and to characterize the overall visibility in the horizontal distribution dataset, visibility score was averaged, then rounded to the nearest whole number to eliminate scores that fell between the three original scores, which would have conveyed a greater degree of precision in estimating visibility than was possible.

Seafloor depth (m), as well as platform characteristics, were recorded in the field, or determined in QGIS using data from the Bureau of Ocean and Energy Management (BOEM 2019). Platform characteristics included: seafloor depth (m); age (years); number of other platforms within 1, 2, 3, and 5 km; length of pipeline within 1, 2, 3, and 5 km; distance from shore (km); and number of legs.

Data Analysis

The encounter or non-encounter of fish species was recorded from camera data at each 10-meter depth layer. Encounter/non-encounter data were analyzed in this study instead of abundance data so as to minimize the impact of differing levels of visibility across survey events. For the horizontal distribution analysis, these data were further reduced to encounter/non-encounter at each survey event (i.e. visit to a site). From these data, rare species (encountered in <10% of survey events) were excluded such that further analyses focused on dominant (encountered in > 90% of survey events), very common (encountered in 60 – 90% of survey events), common (encountered in 30 – 59% of survey events), and uncommon species (encountered in 10 – 29% of survey events) (*sensu* Erisman et al. 2011). Sonde measurements were scrutinized to identify and exclude anomalies. Surface measurements were also excluded.

Statistical Analysis

Binomial generalized additive mixed models (GAMMs; Lin and Zhang 1999) were employed to identify the environmental and structural parameters that influence the probability of encounter of each study species in the horizontal and vertical dimensions. Mixed models (GAMMs) rather than GAMs were used because of the repeated measurements at each platform. Although both survey teams followed the same data collection and analysis protocols, it was necessary to integrate the effect of survey team in GAMMs in addition to the random effect of platform, so as to account for slight potential differences in gear deployment between survey teams. Finally, because local visibility conditions can also have an impact on the probability of encountering species around platforms, our GAMMs also integrated a random visibility factor. The effects of survey team and visibility were also treated as random, so that it was not necessary to choose a specific level for these factors when making predictions with GAMMs (Bolker et al. 2009).

To fit binomial GAMMs in this study, we proceeded in several steps. First, a collinearity analysis (Dormann et al. 2013) was carried out. This collinearity analysis consisted of evaluating

the Pearson's correlation coefficients between environmental and structural predictors, as well as between environmental and structural predictors and eastings and northings (i.e., longitude and latitude, both expressed in Universal Transverse Mercator (UTM) coordinates). If the Pearson's correlation coefficient between an environmental or structural predictor and eastings and northings was greater than 0.7 in absolute value, the environmental or structural predictor was excluded from the analysis; and, if the Pearson's correlation coefficient between two predictors was greater than 0.7 in absolute value, one of the two predictors was excluded (Leathwick et al. 2006; Grüss et al. 2018a, 2019). Next, a binomial GAMM with all possible environmental and structural predictors selected after the collinearity analysis was fit to data from each species. The binomial GAMM was then re-fit with only the significant environmental and structural predictors at $\alpha = 0.05$ (Koubbi et al. 2006; Weber and McClatchie 2010; Chagaris et al. 2015) and environmental and structural predictors with estimated degrees of freedom (EDFs) greater than 0.9 (Large et al. 2013), until the final model included only the significant predictors with an EDF greater than 0.9 (Large et al. 2013; Grüss et al. 2018a, 2019).

To understand parameters influencing the horizontal distribution patterns of fishes associated with petroleum platforms, we fitted binomial 'horizontal distribution GAMMs' of the form:

$$g(\eta) = t2(X,Y) + s(x_1) + s(x_2) + \cdots + s(x_n) + visibility + platform + survey\ team \quad (1)$$

Where η is the probability of encounter of a given species; g is a logit link function between η and each predictor; $t2(X,Y)$ is a tensor product smooth (Wood et al. 2013) fitted to eastings and northings, i.e., the fixed effect of geographic position; x_1, x_2, …, x_n are the environmental and structural predictors selected after the collinearity analysis, which are ultimately retained in or removed from the binomial GAMM based on their *p*-value and EDF; *s* is a thin plate regression spline fit to each continuous predictor; and visibility, platform and survey team are factors treated as random effects. All GAMMs were fit using the 'gamm4' package in the R version 3.4.0

environment (Wood and Scheipl 2013). The degree of freedom of each thin plate regression spline was limited to four in order to preserve the interpretability of the relationships estimated by GAMMs (Roberts et al. 2016; Mannocci et al. 2017; Grüss et al. 2018a). The $te(X, Y)$ term accounts for spatial autocorrelation (spatial structure) at a broad scale and usually results in GAMMs explaining a larger proportion of the deviance in the data (Wood 2006; Grüss et al. 2018a).

To understand parameters influencing the vertical distribution patterns of fishes associated with petroleum platforms, we fitted binomial 'vertical distribution GAMMs' similar to the binomial horizontal distribution GAMMs:

$$g(\eta) = t2(X, Y) + s(x_1) + s(x_2) + \cdots + s(x_n) + visibility + (platform/depth\ bin) + survey\ team \quad (2)$$

where the 'depth bin within platforms' nested random effect ($platform/depth\ bin$) accounts for the fact that different depth bins were surveyed within a given petroleum platform (Bates et al. 2014).

The predictions of horizontal distribution and vertical distribution GAMMs were evaluated using two criteria: (1) the area under the receiver operating curve (AUC), which helps gauge the ability of GAMMs to appropriately discriminate between non-encounters and encounters (Hanley and McNeil 1982); and (2) the adjusted R^2 value, which is a measure of the proportion of the deviance in the data explained by GAMMs (Legendre and Legendre 1998). Since it was not possible to split the datasets into test and validation datasets due to the limited number of observations, we adopted an approach similar to that employed in Grüss et al. (2014) and Weijerman et al. (2019) and evaluated all horizontal distribution and vertical distribution GAMMs using the datasets internal to their development. For each study species, 1000 bootstrap datasets were generated by resampling with replacement from the horizontal distribution dataset and 1000 other bootstrap datasets were generated by resampling with replacement from the vertical distribution dataset, and horizontal distribution and vertical distribution GAMMs were then fit to

bootstrapped datasets. After this, the adjusted R^2 and AUC of the horizontal distribution and vertical distribution GAMMs were calculated, and confidence intervals were generated. A given horizontal distribution or vertical distribution GAMM was deemed reasonable if the lower bound of the confidence interval surrounding its AUC was greater than 0.6 (Hanley and McNeil 1982; Swets 1988; Pearce and Ferrier 2000; Rooper et al. 2016) and the lower bound of the confidence interval around its adjusted R^2 was greater than 0.1 (Legendre and Legendre 1998; Grüss et al. 2016).

To assess the importance of significant environmental and structural parameters in explaining the probability of encounter of each study species, an index of relative importance was calculated for these parameters (Thuiller et al. 2012; Grüss et al. 2019). Specifically, the predictions of the binomial GAMMs fitted earlier using Equations 1 and 2 (referred to as 'full GAMMs') were compared with the predictions of binomial GAMMs after random permutation of the values of the environmental or structural predictor of interest within the dataset fed into GAMMs (referred to as 'random GAMMs'); one minus the Pearson's correlation coefficient between the predictions of the random GAMM and the predictions of the full GAM indicates the relative importance of the environmental or structural parameter of interest in explaining fish probability of encounter (Thuiller et al. 2012; Grüss et al. 2019).

RESULTS

Environmental and Structural Predictors and Species Retained for Analyses

With respect to horizontal distribution GAMMs, the Pearson's correlation coefficients between each environmental and structural predictor and eastings and northings were all smaller than 0.7 in absolute value (Appendix 2). Moreover, the Pearson's correlation coefficients between temperature, salinity, DO concentration, minimum DO concentration, platform age, number of legs, seafloor depth, and distance from shore were all smaller than 0.7 in absolute value (Appendix 2) and were therefore deemed suitable for inclusion in horizontal distribution GAMMs. On the other hand, the Pearson's correlation coefficients between number of platforms and length of

pipeline within 1, 2, 3 and 5 km were all greater than 0.7 in absolute value. The number of platforms within 5 km was selected for inclusion in horizontal distribution GAMMs over the other pipeline and platform vicinity variables based upon preliminary correlations with the encounter or non-encounter of the study species.

With respect to vertical distribution GAMMs, the Pearson's correlation coefficients between each environmental and structural predictor and eastings and northings were all smaller than 0.7 in absolute value (Appendix 2). Moreover, the Pearson's correlation coefficients between salinity, DO concentration, temperature, and seafloor depth were smaller than 0.7 in absolute value (Appendix 2) and were therefore included as smoothed predictors in vertical distribution GAMMs.

Seventeen species were encountered in 10% or greater of survey events: Red Snapper, Blue Runner, Crevalle Jack (*Caranx hippos*), Atlantic Spadefish, Bermuda Chub (*Kyphosus sectatrix*), Great Barracuda (*Sphraena barracuda*), Gray Snapper (*Lutjanus griseus*), Greater Amberjack, Almaco Jack (*Seriola rivoliana*), Cobia (*Rachycentron canadum*), Rainbow Runner (*Elagatis bipinnulata*), Vermilion Snapper (*Rhomboplites aurorubens*), Gray Triggerfish, King Mackerel (*Scomberomorus cavalla*), Atlantic Bumper (*Chloroscombrus chrysurus*), Horse-Eye Jack (*Caranx latus*), and Lookdown (*Selene vomer*). For each species, there were 114 encounter/non-encounter records in the horizontal distribution dataset, and 502 encounter/non-encounter records in the vertical distribution dataset. Number and percent of encounters for individual species are provided in Table 3.1.

Table 3.1: Number of encounters (percentage in parentheses) of fish species observed on petroleum platforms in the northern Gulf of Mexico in either the horizontal or vertical data sets.

Species	Horizontal distribution dataset	Vertical distribution dataset
Almaco Jack (*Seriola rivoliana*)	38 (33%)	72 (14%)
Atlantic Bumper (*Chloroscombrus chrysurus*)	18 (16%)	37 (7%)
Atlantic Spadefish (*Chaetodipterus faber*)	55 (48%)	105 (21%)
Bermuda Chub (*Kyphosus sectatrix*)	55 (48%)	111 (22%)
Blue Runner (*Caranx crysos*)	83 (73%)	187 (37%)
Cobia (*Rachycentron canadum*)	26 (23%)	32 (6%)
Crevalle Jack (*Caranx hippos*)	61 (54%)	103 (21%)
Gray Snapper (*Lutjanus griseus*)	48 (42%)	99 (20%)
Gray Triggerfish (*Balistes capriscus*)	20 (18%)	28 (6%)
Greater Amberjack (*Seriola dumerili*)	48 (42%)	129 (26%)
Great Barracuda (*Sphyraena barracuda*)	50 (44%)	96 (19%)
Horse-Eye Jack (*Caranx latus*)	11 (10%)	18 (4%)
King Mackerel (*Scomberomorus cavalla*)	19 (17%)	26 (5%)
Lookdown (*Selene vomer*)	11 (10%)	15 (3%)
Rainbow Runner (*Elagatis bipinnulata*)	21 (18%)	35 (7%)
Red Snapper (*Lutjanus campechanus*)	89 (78%)	230 (46%)
Vermilion Snapper (*Rhomboplites aurorubens*)	21 (18%)	33 (7%)

Overview of the Environmental Parameters and Platform Parameters Retained for Analyses

In the horizontal distribution dataset, average DO concentration ranged from 1.98 to 6.91 mg/L (30.37 – 101.02 % saturation; Table 3.2). Water was hypoxic (DO < 2.0 mg/L) on average on one survey event. Water was below 50% DO saturation on average on two survey events. Minimum DO concentration ranged from 0.30 mg/L to 6.37 mg/L. Average salinity ranged from 25.85 to 37.60 psu. Average temperature ranged from 21.48 to 30.58 °C. Platform age ranged from

3.85 to 62.59 years. Seafloor depth ranged from 10.67 to 142.34 m. Number of platforms within five km of the focal platform ranged from 0 to 31. Distance from shore ranged from 10.33 to 163.90 km. Finally, the number of legs on study platforms ranged from 1 to 20 (Table 3.2).

Table 3.2: Summary statistics for predictors in the horizontal distribution data set. For environmental parameters, values in the horizontal distribution data set represent averages across the entire water column for each combination of study platform, survey team, and sampling date.

Parameter	Lowest value	Highest value	Range	Mean	Standard deviation
Dissolved oxygen (mg/L)	1.98	6.91	4.93	5.73	0.85
Distance from shore (km)	10.33	163.90	153.57	76.30	42.10
Minimum dissolved oxygen (mg/L)	0.30	6.37	6.07	4.44	1.53
Number of legs	1	20	19	5.24	3.58
Number of platforms within 5 km	0	31	31	4.39	6.93
Platform age (years)	3.85	62.59	58.74	28.87	15.31
Salinity (psu)	25.85	37.60	11.75	33.96	2.72
Seafloor depth (m)	10.67	142.34	131.67	40.97	22.56
Temperature (°C)	21.48	30.58	9.1	26.52	1.95

In the vertical distribution dataset, average DO concentration ranged from 0.60 to 9.29 mg/L (9.22 – 130.70 % saturation; Table 3.3). Water layers were hypoxic on average eight times. Water layers with less than 50% DO saturation were observed 18 times. Average salinity ranged from 0.13 – 38.96 psu. Average temperature ranged from 18.35 – 31.19 °C. Finally, as indicated previously, seafloor depth ranged from 10.67 to 142.34 m (Table 3.3).

Table 3.3: Summary statistics for predictors in the vertical distribution data set. For environmental parameters, values in the vertical distribution data set represent averages within 10-m depth intervals for each combination of study platform, survey team, and sampling date.

Parameter	Lowest value	Highest value	Range	Mean	Standard deviation
Dissolved oxygen (mg/L)	0.60	9.29	8.69	5.91	1.12
Salinity (psu)	0.13	38.96	38.83	33.88	4.59
Seafloor depth (m)	10.67	142.34	131.67	40.97	22.56
Temperature (°C)	18.35	31.19	12.84	26.45	3.13

GAMM Results

The horizontal and vertical distributions of the majority of the study species (11/17 species in horizontal distribution GAMMs, 9/17 species in vertical distribution GAMMs) were not found to be influenced by any of the environmental and structural parameters included in GAMMs (i.e. no modeled parameters showed statistically significant effects). For horizontal distribution GAMMs, these species were Almaco Jack, Atlantic Bumper, Atlantic Spadefish, Gray Snapper, Gray Triggerfish, Great Barracuda, Horse-Eye Jack, King Mackerel, Lookdown, and Rainbow Runner. For vertical distribution GAMMs, these species were Almaco Jack, Atlantic Bumper, Cobia, Gray Snapper, Gray Triggerfish, Horse-Eye Jack, King Mackerel, Lookdown, and Rainbow Runner.

All GAMMs for species that were influenced by environmental or structural parameters passed the validation test based on their adjusted-R^2 and AUC values, except for the vertical distribution GAMMs for Great Barracuda, Crevalle Jack, and Vermilion Snapper, whose predictions cannot be deemed reasonable and hence they were excluded from further consideration. Thus, results from the validation test indicate that the vertical distributions of 12 species were not influenced by modeled parameters, instead of the 9 originally deemed so from the significance of parameters alone. Temperature, minimum DO concentration, platform age, seafloor depth, and number of legs did not affect the horizontal distribution of any of the study

species. Significant results from models that passed the validation test are grouped by parameter below and shown in Figs. 3.2-7.

Salinity

Salinity was found to influence the horizontal distribution of Bermuda Chub and Red Snapper (Table 3.4). These species exhibited increasing probability of encounter in the horizontal dimension with increasing salinity, although, for Red Snapper, this effect held to approximately 31 psu, after which the probability of encounter decreased with increasing salinity (Bermuda Chub: Fig. 3.2b; Red Snapper: Fig. 3.4b). Salinity was the second most important parameter in explaining probability of encounter in the horizontal dimension for both Bermuda Chub (Fig. 3.2c) and Red Snapper (Fig. 3.4c).

Table 3.4: Fish species influenced by environmental and structural predictors retained in the final horizontal distribution GAMMs. Significant smoothed predictors for each species are ordered by relative importance (see Figures 2–4). Statistics are presented for fully reliably GAMMs, which were deemed so if the lower bound of the confidence interval around their adjusted *R*2 was greater than 0.1 and the lower bound of the confidence interval around their area under the receiver operating curve (AUC) was greater than 0.6. Abbreviations are as follows: EDF = estimated degrees of freedom.

Species	Significant Predictors ($p < 0.05$, EDF > 0.9)	Adjusted R^2 *(CI)*	AUC *(CI)*
Bermuda Chub	Distance from Shore, Salinity	0.441 *(0.294 – 0.621)*	0.893 *(0.838 – 0.964)*
Blue Runner	Number of Platforms within 5 km	0.280 *(0.129 – 0.473)*	0.843 *(0.770 – 0.928)*
Crevalle Jack	Number of Platforms within 5 km	0.246 *(0.113 – 0.393)*	0.786 *(0.706 – 0.872)*
Greater Amberjack	Distance from Shore	0.659 *(0.511 – 0.839)*	0.961 *(0.933 – 1.00)*
Red Snapper	Dissolved Oxygen, Salinity	0.652 *(0.495 – 0.844)*	0.973 *(0.952 – 1.00)*
Vermilion Snapper	Distance from Shore	0.332 *(0.189 – 0.531)*	0.893 *(0.840 – 0.958)*

Salinity was found to influence the vertical distribution of Greater Amberjack and Red Snapper (Table 3.5). Both of these species exhibited an increasing probability of encounter in the vertical dimension with increasing salinity. Salinity was the most important parameter in explaining probability of encounter in the vertical dimension for Red Snapper (Fig. 3.7a), and the

second most important parameter in explaining probability of encounter in the vertical dimension for Greater Amberjack (Fig. 3.6e).

Table 3.5: Fish species influenced by environmental and structural predictors retained in the final vertical distribution GAMMs. Significant smoothed predictors for each species are ordered by relative importance (see Figures 5, 6). Statistics are presented for these fully reliably GAMMs, which were deemed so if the lower bound of the confidence interval around their adjusted *R*2 was greater than 0.1 and the lower bound of the confidence interval around their area under the receiver operating curve (AUC) was greater than 0.6. Abbreviations are as follows: EDF = estimated degrees of freedom.

Species	Significant Predictors ($p < 0.05$, EDF > 0.9)	Adjusted R^2 *(CI)*	AUC *(CI)*
Atlantic Spadefish	Temperature	0.213 *(0.136 – 0.298)*	0.822 *(0.781 – 0.866)*
Bermuda Chub	Temperature	0.291 *(0.225 – 0.359)*	0.882 *(0.853 – 0.913)*
Blue Runner	Temperature	0.210 *(0.150 – 0.274)*	0.788 *(0.751 – 0.831)*
Greater Amberjack	Temperature, Salinity	0.420 *(0.344 – 0.495)*	0.910 *(0.884 – 0.936)*
Red Snapper	Salinity, Temperature Seafloor Depth, Dissolved Oxygen	0.340 *(0.267 – 0.414)*	0.844 *(0.812 – 0.881)*

DO concentration

DO concentration was found to influence the horizontal distribution of Red Snapper. The probability of encounter of Red Snapper in the horizontal dimension was predicted to increase with increasing DO concentration (Table 3.4, Fig. 3.4a). DO concentration was the most important

parameter in explaining the probability of encounter of Red Snapper in the horizontal dimension (Fig. 3.4c).

DO concentration was also found to influence the vertical distribution of Greater Amberjack and Red Snapper (Table 3.5). Both of these species exhibited increasing probability of encounter in the vertical dimension with increasing DO concentration (Greater Amberjack: Fig. 3.6b; Red Snapper: Fig. 3.7b). DO concentration was the fourth most important parameter in explaining probability of encounter in the vertical dimension for Greater Amberjack (Fig. 3.6c), and the third most important parameter in explaining probability of encounter in the vertical dimension for Red Snapper (Fig. 3.7d).

Temperature

Temperature was found to influence the vertical distribution of Atlantic Spadefish, Bermuda Chub, Blue Runner, Greater Amberjack and Red Snapper (Table 3.5). Atlantic Spadefish exhibited an increasing probability of encounter in the vertical domain with increasing temperature (Fig. 3.5a). Bermuda Chub and Blue Runner also exhibited an increasing probability of encounter in the vertical domain with increasing temperature until approximately 28 °C, after which it largely did not change for Bermuda Chub (Fig. 3.5c), but decreased for Blue Runner (Fig 6a). Greater Amberjack and Red Snapper exhibited increasing probability of encounter with increasing temperature until approximately 25 °C, after which it decreased with increasing temperature (Greater Amberjack: Fig. 3.6c; Red Snapper: Fig 7c). Temperature was the sole significant parameter in vertical distribution GAMMs for Atlantic Spadefish, Bermuda Chub, and Blue Runner (Table 3.5). Temperature was the most important parameter in explaining probability of encounter for Greater Amberjack (Fig. 3.6e), and the second most important parameter for Red Snapper (Fig. 3.7a).

Distance from shore

Distance from Shore was found to influence the horizontal distribution of Bermuda Chub, Greater Amberjack, and Vermilion Snapper (Table 3.4). These species exhibited an increasing probability of encounter in the horizontal dimension with increasing distance from shore, although this effect holds until approximately 115 km from shore for Greater Amberjack, after which probability of encounter decreases with increasing distance from shore (Bermuda Chub: Fig. 3.2a; Greater Amberjack: Fig. 3.3c; Vermilion Snapper: Fig. 3.4d). Distance from shore was the only significant parameter for Greater Amberjack and Vermilion Snapper (Table 3.4), and was the second most important parameter in explaining probability of encounter in the horizontal dimension for Bermuda Chub (Fig. 3.2c).

Number of platforms within five kilometers

The number of platforms within five kilometers was found to influence the horizontal distribution of Blue Runner and Crevalle Jack (Table 3.4). For both of these species, probability of encounter in the horizontal dimension increased with decreasing number of platforms (Blue Runner: Fig. 3.2d; Crevalle Jack: Fig. 3.3a). Number of platforms within five kilometers was the only significant parameter for both species (Table 3.4).

Seafloor depth

Seafloor depth was found to influence the vertical distribution of Red Snapper. The probability of encounter of Red Snapper in the vertical dimension was predicted to increase with decreasing seafloor depth (Table 3.5, Fig. 3.7d). Seafloor depth was the third most important parameter in explaining the probability of encounter of Red Snapper in the vertical dimension.

Geographic position

Geographic position is not an environmental or a structural predictor, and is included in GAMMs to account for spatial structure at a broad scale. However, geographic position accounts for variables that are not explicitly included in GAMMs but can have an influence on fish

probability of encounter (Wood 2006; Grüss et al. 2018a). Therefore, we also briefly report GAMM results with respect to the effect of geographic position for models that passed the evaluation test, and include eastings and northings in relative importance plots to assess the effects of significant environmental and structural parameters relative to variation in probability of encounter unexplained by environmental and structural parameters but captured by the geographic position term.

Geographic position was the sole significant parameter in the horizontal distribution GAMMs of Almaco Jack, Atlantic Bumper, and Great Barracuda. Geographic position was also a significant parameter in the horizontal distribution GAMMs of Blue Runner, Crevalle Jack, Greater Amberjack, and Vermilion Snapper. Moreover, geographic position was a significant parameter in the vertical distribution GAMMs of Atlantic Spadefish and Blue Runner.

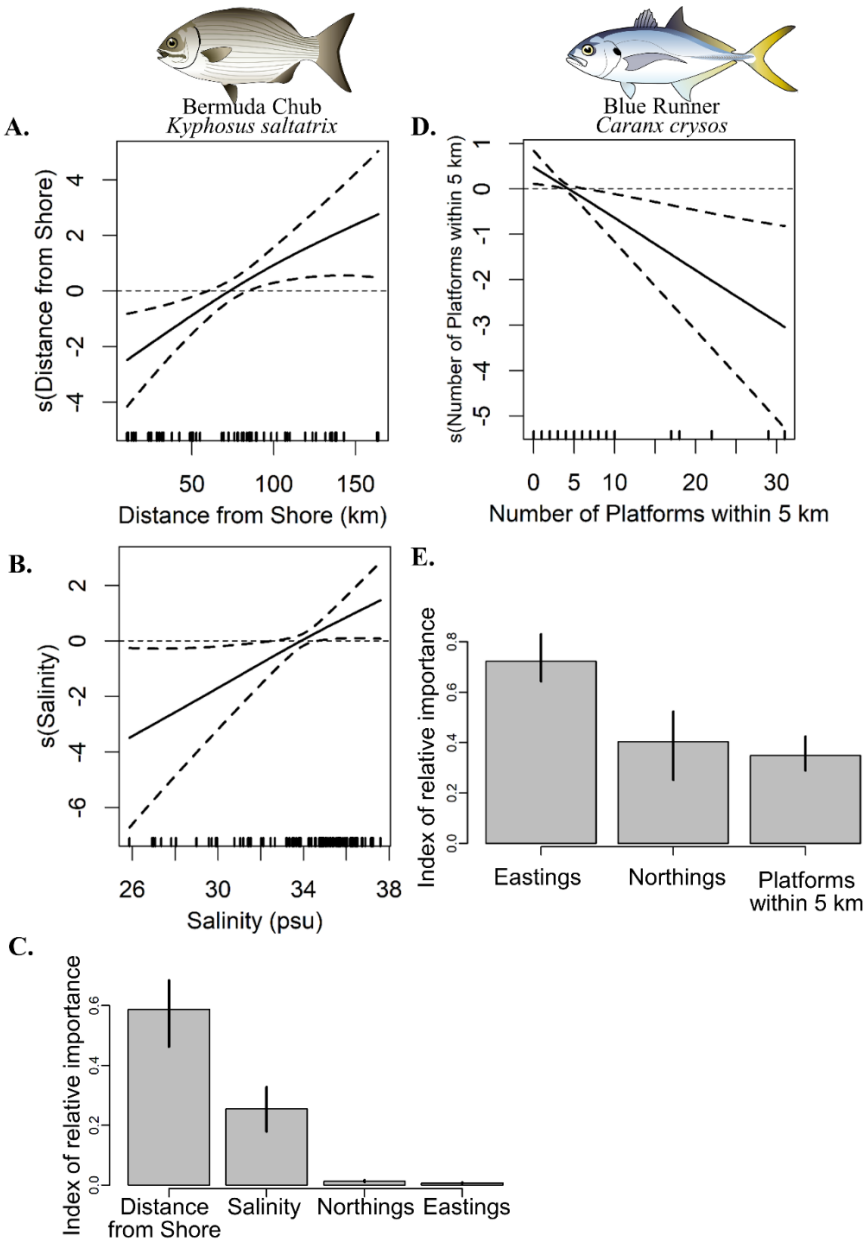

Figure 3.2: Fits of the horizontal distribution GAMMs of Bermuda Chub and Blue Runner and the relative importance of predictors predicted by these GAMMs, including (A) the marginal effect of distance from shore on the probability of encountering Bermuda Chub in the horizontal dimension, (B) the marginal effect of salinity on the probability of encountering Bermuda Chub in the horizontal dimension, (C) the relative importance of predictors predicted by the Bermuda Chub horizontal distribution GAMM, (D) the marginal effect of the number of platforms within 5 km on the probability of encountering Blue Runner in the horizontal dimension, and (E) the relative importance of predictors predicted by the Blue Runner horizontal distribution GAMM. The dashed line at zero on the *y*-axis of panels (A), (B), and (D) represents a neutral marginal effect for reference, and the tick marks on the *x*-axis represent observed values of the predictor.

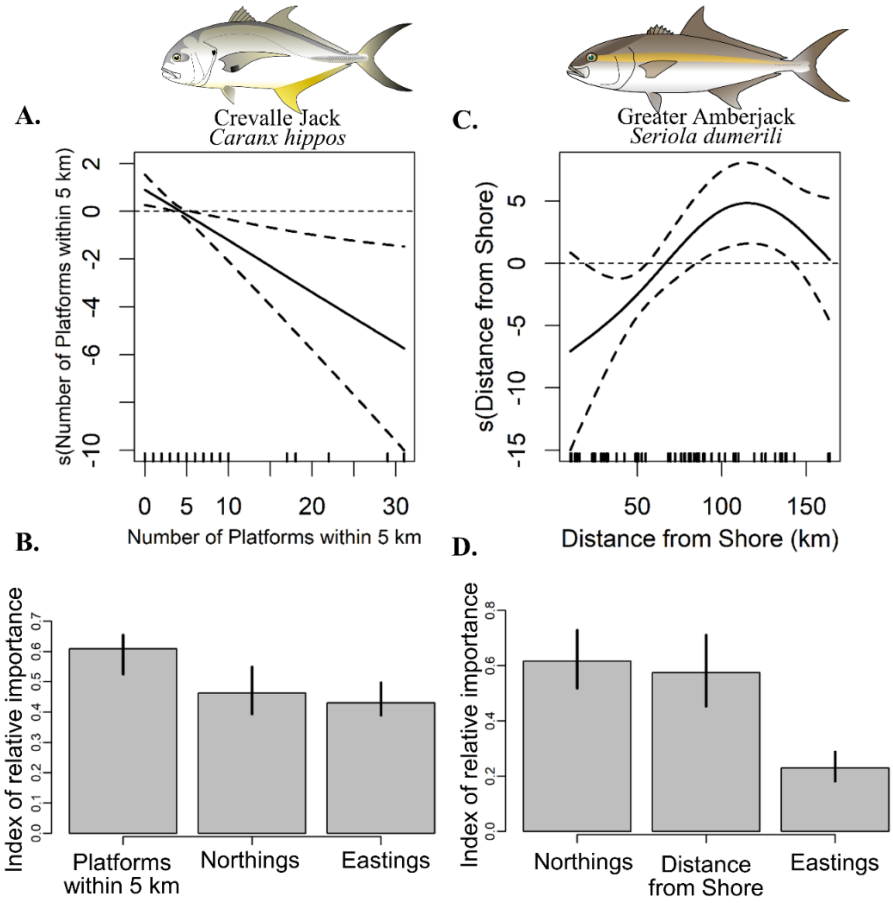

Figure 3.3: Fits of the horizontal distribution GAMMs of Crevalle Jack and Greater Amberjack and the relative importance of predictors predicted by these GAMMs, including (A) the marginal effect of the number of platforms within 5 km on the probability of encountering Crevalle Jack in the horizontal dimension, (B) the relative importance of predictors predicted by the Crevalle Jack horizontal distribution GAMM, (C) the marginal effect of distance from shore on the probability of encountering Greater Amberjack in the horizontal dimension, and (D) the relative importance of predictors predicted by the Greater Amberjack horizontal distribution GAMM. The dashed line at zero on the *y*-axis of panels (A) and (C) represents a neutral marginal effect for reference, and the tick marks on the *x*-axis represent observed values of the predictor.

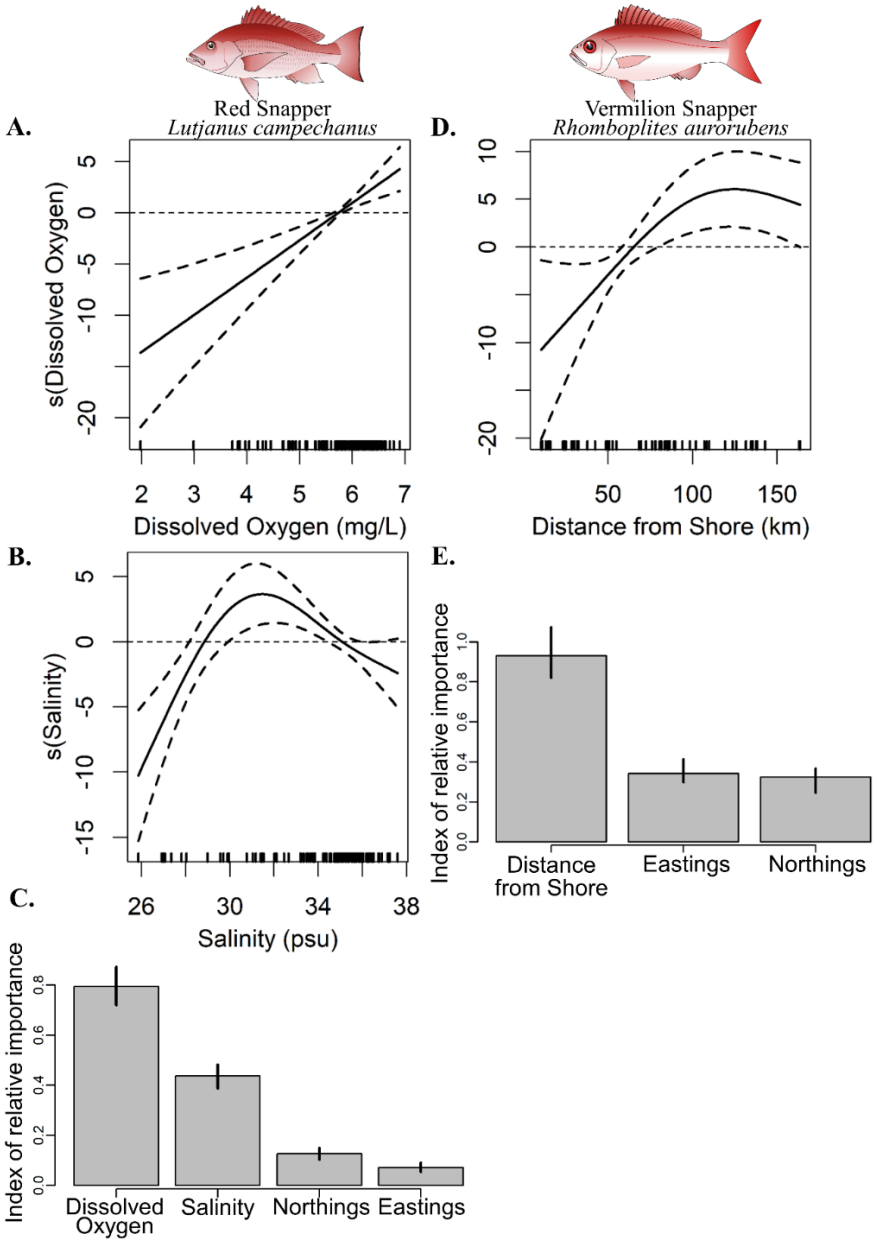

Figure 3.4: Fits of the horizontal distribution GAMMs of Red Snapper and Vermilion Snapper and the relative importance of predictors predicted by these GAMMs including (A) the marginal effect of dissolved oxygen concentration on the probability of encountering Red Snapper in the horizontal dimension, (B) the marginal effect of salinity on the probability of encountering Red Snapper in the horizontal dimension, (C) the relative importance of predictors predicted by the Red Snapper horizontal distribution GAMM, (D) the marginal effect of distance from shore on the probability of encountering Vermilion Snapper in the horizontal dimension, and (E) the relative importance of predictors predicted by the Vermilion Snapper horizontal distribution GAMM. The dashed line at zero on the *y*-axis of panels (A), (B), and (D) represents a neutral marginal effect for reference, and the tick marks on the *x*-axis represent observed values of the predictor.

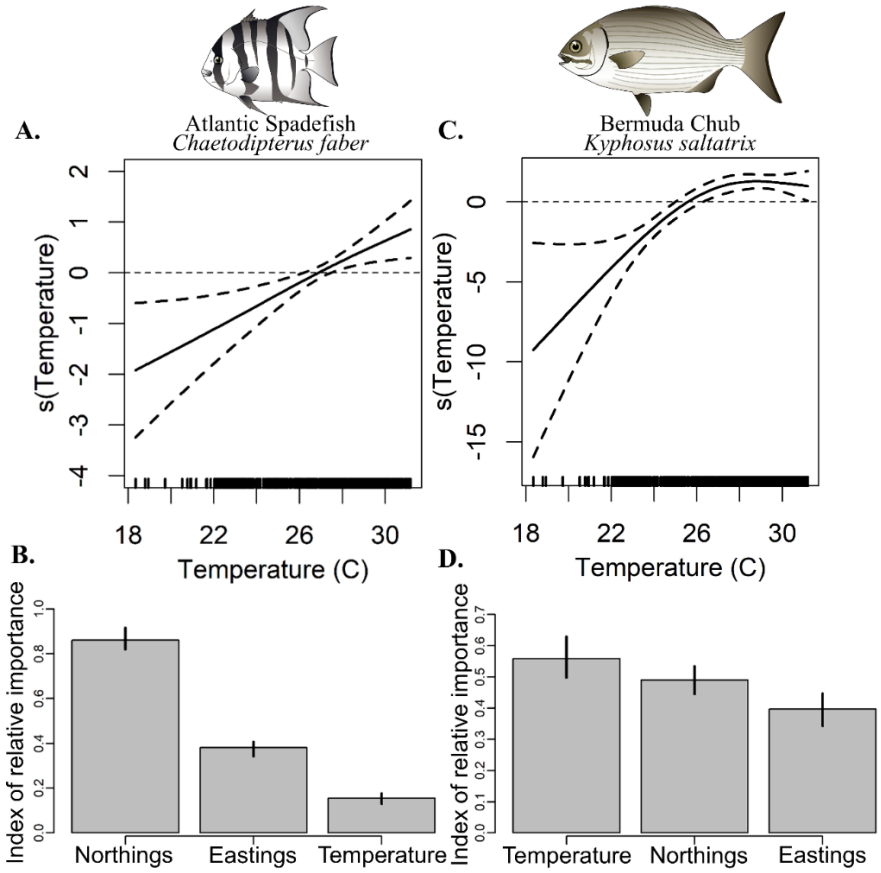

Figure 3.5: Fits of the vertical distribution GAMMs of Atlantic Spadefish and Bermuda Chub and the relative importance of predictors predicted by these GAMMs, including (A) the marginal effect of temperature on the probability of encountering Atlantic Spadefish in the vertical dimension, (B) the relative importance of predictors predicted by the Atlantic Spadefish vertical distribution GAMM, (C) the marginal effect of temperature on the probability of encountering Bermuda Chub in the vertical dimension, and (D) the relative importance of predictors predicted by the Atlantic Spadefish vertical distribution GAMM. The dashed line at zero on the *y*-axis of panels (A) and (C) represents a neutral marginal effect for reference, and the tick marks on the *x*-axis represent observed values of the predictor. Please note the different *y*-axis scales in panels (A) and (C).

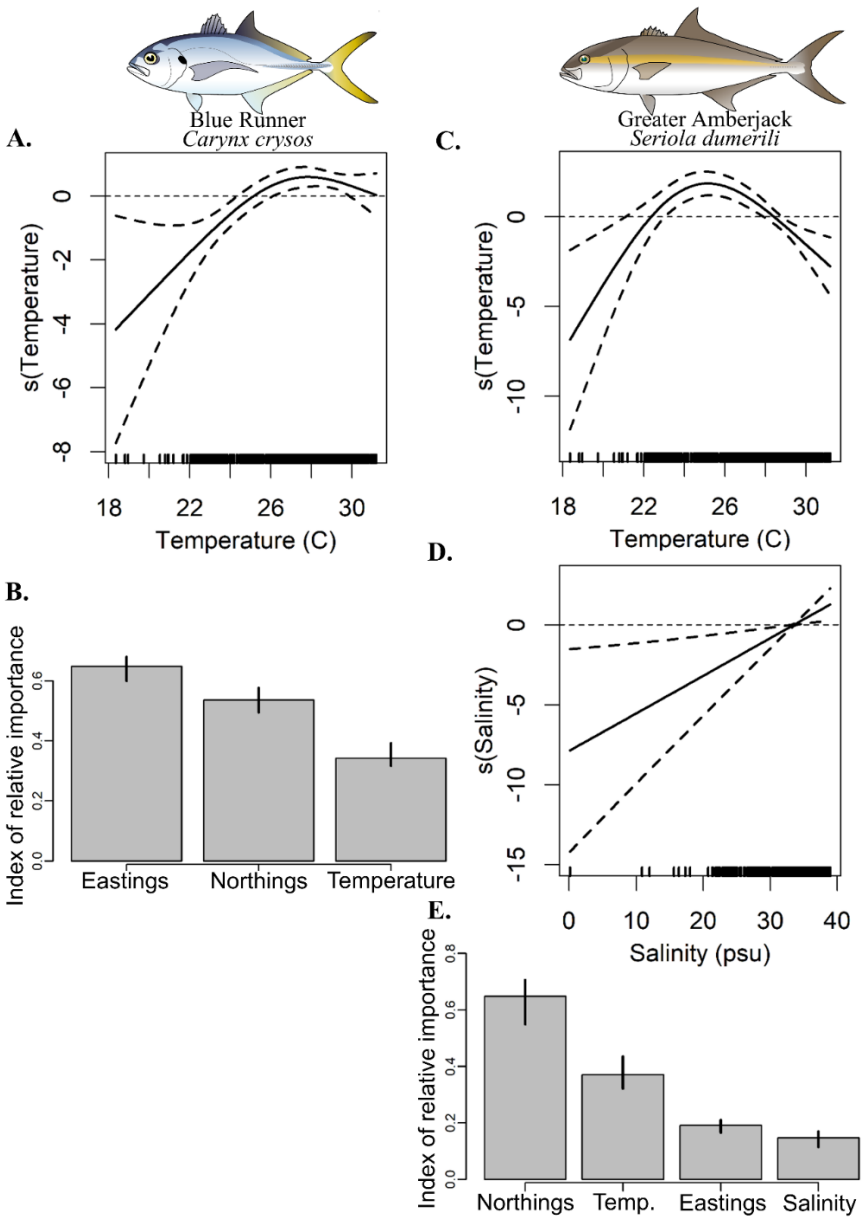

Figure 3.6: Fits of the vertical distribution GAMMs of Blue Runner and Greater Amberjack and the relative importance of predictors predicted by these GAMMs, including (A) the marginal effect of temperature on the probability of encountering Blue Runner in the vertical dimension, (B) the relative importance of predictors predicted by the Blue Runner vertical distribution GAMM, (C) the marginal effect of temperature on the probability of encountering Greater Amberjack in the vertical dimension, (D) the marginal effect of salinity on the probability of encountering Greater Amberjack in the vertical dimension, and (E) the relative importance of predictors predicted by the Greater Amberjack vertical distribution GAMM. The dashed line at zero on the *y*-axis of panels (A), (C), and (D) represents a neutral marginal effect for reference, and the tick marks on the *x*-axis represent observed values of the predictor. Please note the different *y*-axis scales of panels (A) and (C).

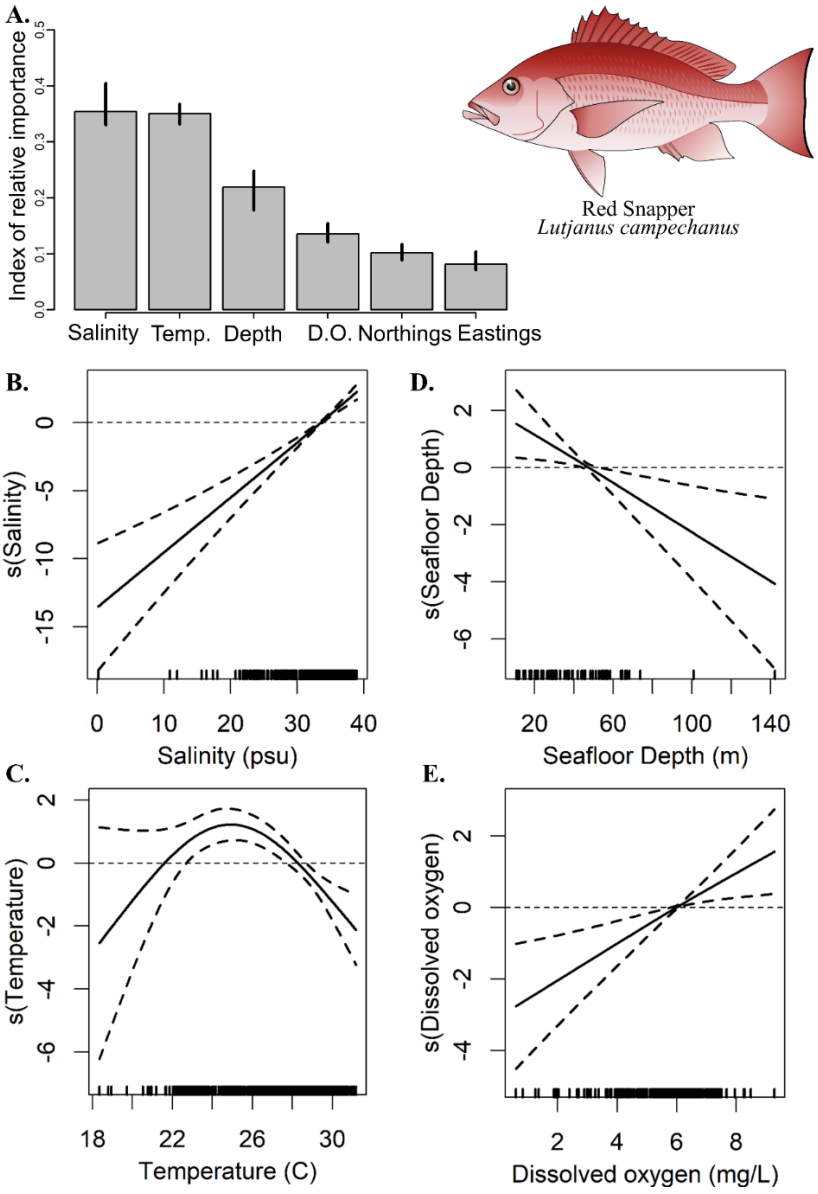

Figure 3.7: Fits of the vertical distribution GAMM of Red Snapper and the relative importance of predictors predicted by this GAMM, including **(A)** the relative importance of predictors predicted by the Red Snapper vertical distribution GAMM (depth refers to seafloor depth, and D.O. refers to dissolved oxygen concentration), **(B)** the marginal effect of salinity on the probability of encountering Red Snapper in the vertical dimension, **(C)** the marginal effect of temperature on the probability of encountering Red Snapper in the vertical dimension, **(D)** the marginal effect of seafloor depth on the probability of encountering Red Snapper in the vertical dimension, and **(E)** the marginal effect of dissolved oxygen concentration on the probability of encountering Red Snapper in the vertical dimension. The dashed line at zero on the *y*-axis of panels (B), (C), (D), and (E) represents a neutral marginal effect for reference, and the tick marks on the *x*-axis represent observed values of the predictor.

DISCUSSION

Platform-associated fishes are exposed to a wide range of environmental conditions on the thousands of platforms that exist throughout the GOM. These platforms are diverse in their size and complexity, yet all represent important habitat for fishes and help support fisheries (Gallaway and Lewbel 1982; Stanley and Wilson 2000; Cowan and Rose 2016). Moreover, platforms of the GOM are often found in areas where other reef habitat, particularly natural reef habitat, is lacking (Gallaway and Cole 1998). We conducted 114 SRV drop-camera surveys of 54 platforms throughout the GOM, generating spatially extensive and depth-resolved data that allowed us to advance the conclusions of seminal work on platform-associated fishes and focus on species-specific drivers. By fitting two sets of GAMMs to encounter and non-encounter records of fishes from these data, we concluded that several species, including Atlantic Spadefish, Bermuda Chub, Blue Runner, Crevalle Jack, Greater Amberjack, Red Snapper, and Vermilion Snapper, exhibit distribution patterns in GOM platform habitat that are driven by environmental and structural variables. The other study species were present at platforms across a wide range of environmental conditions and platform characteristics. Understanding the drivers – or lack thereof – of the horizontal and vertical distribution patterns of platform-associated species may aid in stratification of sampling effort for future studies and assessments, facilitating predictions of how their future distributions might change in response to climate change and altered habitat availability, and quantifying the consequences of such changes for the fisheries that operate around petroleum platforms.

Species whose distribution patterns were not explained by environmental and structural predictors explicitly included in GAMMs, or those that did not exhibit spatial structure in distribution patterns, may remain in sub-optimal environmental conditions to take advantage of the high-relief of platform habitat, regardless of specific platform characteristics. Platform-type structures are associated with increased interactions between conspecifics and prey organisms, a balance of resting and foraging habitat, and increased larval settlement opportunities (Fréon and Dagorn 2000; Hernández-Arana et al. 2003; Genin 2004). The GOM is prone to acute and seasonal

shifts in environmental conditions, and it is likely that many species that thrive in this dynamic region have evolved to tolerate a wide range of environmental conditions without undergoing significant physiological stress. This tolerance would enable them to take advantage of the benefits associated with limited high-relief habitat. Thus, habitat limitation likely constrains the distributions of adult populations of reef-associated GOM fishes more than environmental conditions, at least where platform habitat is concerned. Further research is needed to determine species-specific tolerance levels to potential stressors, but we would expect physiological measurements to align with model outputs if optimality theory is acting at the scale of this study (e.g. Red Snapper would have the lowest tolerance to hypoxia among the study species).

It is possible that variation in probability of encounter not explained by the environmental and structural parameters but partly captured by the geographic position term could be explained by oceanic currents and circulation (i.e. 'exposure to Caribbean water masses', Gallaway and Lewbell 1982), or the distribution of planktonic or other non-focal predator or prey organisms. Indeed, the distribution of frontal zones, with their high biomass of phytoplankton and zooplankton (Govoni et al. 1989; Grimes and Finucane 1991), may be influential in explaining the distribution patterns of many of our study species. The distribution of other non-platform reef areas, natural or artificial, may also be important for explaining the distribution patterns of many of our study fish species, considering that proximity to reefs has been linked to the biomass abundance of fishes (Strelcheck et al. 2005; Froehlich and Kline 2015). As with distance from shore, larval dispersal may have a large influence in this area as well (Cowen and Sponaugle 2009). It was not possible to quantify these parameters for this study, but this should ideally be attempted in future studies.

Despite the lack of influence of modeled parameters on the distribution of the majority of study species, the distributions of eight species were influenced by environmental and structural parameters across the vertical and horizontal dimensions (Tables 3.4 and 3.5). Among the environmental and structural parameters that were explicitly included in GAMMs, temperature was found to be the most frequently important parameter in explaining probability of encounter for the study species, although it was only influential in the vertical dimension (for five species;

Table 3.5). Small deviations from thermal optima can have measurable effects on fish physiological performance (Payne et al. 2016), and our results suggest that fishes may be shifting their vertical distributions to take advantage of favorable thermal conditions. The high relief of platform habitat allows them to do this while remaining structure-associated – a contrast with the majority of other types of reef habitat in the GOM. The temperatures associated with the highest probability of occurrence for the five species influenced by temperature typically occurred in the upper 30-40 m of the water column at a given platform (Appendix 2). On platforms in sufficient depths, it may be expected that these species would start inhabiting cooler and deeper waters as water temperatures rise with climate change (Dulvy et al. 2008).

Salinity stress can negatively impact fishes in a variety of ways through increased energetic costs of osmoregulation (Boeuf and Payan 2001), and was influential in explaining the horizontal and vertical distributions of two species in each dimension (Tables 3.4 and 3.5). Unsurprisingly, salinity has previously been suggested to influence the structure of platform-associated fish assemblages (Gallaway 1981; Gallaway and Lewbell 1982). We suspect that the effects of salinity on the vertical distribution found in this study are largely driven by the particularly low salinity in the top 10-meter depth layer at some sites (Appendix 2). As evidenced by the wide range of salinities observed in this depth layer across sites (Appendix 2), hyposaline conditions may be ephemeral; therefore, there would be few reasons for organisms to undergo the energetically-costly process of adapting to them. However, it should be noted that we encountered relatively few depth layers with extremely low salinity – all of which were encountered in the first 10-m depth layer (Appendix 2) – so it would be beneficial for future studies to examine these relationships further.

Red Snapper was the only species that we found to be influenced by an environmental parameter other than temperature or salinity (Tables 3.4 and 3.5). DO concentration influenced the probability of encounter of Red Snapper in both the horizontal and vertical dimensions (Tables 3.4 and 3.5). Previous studies of Red Snapper ecology in non-platform habitats indicated that DO concentration had a moderate to large effect on the abundance and horizontal distribution of this

species (Szedlmayer and Shipp 1994; Szedlmayer and Mudrak 2014; Switzer et al. 2015). DO concentration has also been reported to constrain Red Snapper vertical distribution on petroleum platforms (Stanley and Wilson 2004; Reeves et al. 2018; Munnelly et al. 2019). Indeed, Gallaway et al. (1999) concluded that ideal habitat for juvenile Red Snapper would have DO concentrations greater than 5 mg/L. Therefore, we suspect that the climate change-induced increase in the intensity and scale of the hypoxic 'dead zone' that occurs in waters offshore of Louisiana (Justić et al. 1996) may constrain the amount of platform habitat available to Red Snapper.

Petroleum platforms in the GOM are surrounded by a highly variable number of other platforms (Fig. 3.1). The probability of encounter of Crevalle Jack in the horizontal dimension was found to be significantly influenced by the number of other platforms within five kilometers. Although Crevalle Jack are thought to exhibit low fidelity to platforms, their prey are attracted to these structures (Klima and Wickham, 1971) and are likely to exist at higher densities around platforms that are far away from similar habitat (Bohnsack 1989). Since the distribution of Blue Runner (a common prey species; Saloman and Naughton 1984) was also found to be affected by the number of platforms within five kilometers in this study, it is possible that the distribution of Crevalle Jack is tracking that of Blue Runner. Blue Runner establish home ranges around single platforms with mean daily ranges between 372 and 2,202 m^2 (Brown et al. 2010), further supporting their residence on isolated platforms despite pelagic swimming behavior. In general, studies have found that reef fish abundance and biomass are highest on artificial reefs that are intermediate to long distances away from other reefs (Strelcheck et al. 2005; Froehlich and Kline 2015).

For Bermuda Chub, Greater Amberjack, and Vermilion Snapper, probability of encounter in the horizontal dimension increased with increasing distance from shore, although this effect was reduced at distances greater than approximately 115 km for Greater Amberjack and Vermilion Snapper (Table 3.4; Figs. 2a, 3c, and 4d). The lower fishing pressure that areas located long distances from shore are thought to experience (Sampson 1992; Caddy and Carocci 1999; McCluskey and Lewison 2008) could contribute to explaining this pattern for Greater Amberjack

and Vermilion Snapper, which are important fishery species in the GOM. Fishing lessens biodiversity (Pauly et al. 2002), and the 'bluewater' platforms (*sensu* Gallaway and Lewbell 1982), which are typically located far away from shore, are thought to possess more diverse assemblages of 'tropical' fishes compared to their counterparts located further inshore (*sensu* Gallaway and Lewbell 1982). The high diversity of potential prey organisms at bluewater platforms could contribute to explaining the higher probability of encounter of these species, although the biomass of algae and biofouling organisms in bluewater areas is lower than in the other zones (Gallaway and Lewbell 1982), which would not be beneficial for the omnivorous Bermuda Chub. However, an alternate explanation may be that the influence of distance from shore is actually reflecting larval dispersal patterns (Cowen and Sponaugle 2009). Given the effects of distance from shore and the number of other platforms within five kilometers, removal of platforms in offshore areas could restrict the distributions of Bermuda Chub, Greater Amberjack, and Vermilion Snapper (Table 3.4; Figs. 2a, 3c and 4d), while lower densities of platforms overall may facilitate the expansion of the distributions of Blue Runner and Crevalle Jack (Table 3.4 and Figs. 2d and 3a).

Interestingly, the age and complexity (here represented as number of legs) of the study platforms were not found to be significant predictors of the horizontal or vertical distribution of any study species. This is not typically the case for other types of artificial reefs. Typically, more complex artificial reefs are home to more abundant and diverse communities of fishes (Almany 2004; Lingo and Szedlmayer 2006). It is possible that the substantial vertical relief of petroleum platforms provides sufficient high-quality habitat such that the age and complexity of the platform is less important than in other artificial reefs, which typically exhibit much lower relief. Platforms are often found in areas devoid of similar natural habitat, making them the best available reef habitat in some areas (Gallaway and Cole 1998). Another possible explanation of the lack of influence of platform age is that biofouling communities on platforms may not reach a true 'climax community' due to the dynamic nature of the waters that platforms are found in (George and Thomas 1979).

There are many advantages of using camera surveys to gather distributional information for reef fishes, chief among them being the ability to collect data at different depths (Koenig and Stallings 2015; Grüss et al. 2018b). However, camera monitoring programs are often limited in the number of data points and periods sampled when compared with other GOM monitoring programs such as vertical line monitoring programs around platforms (Rester et al. 2017). Local visibility can also be a limitation of camera studies. While it was not possible to quantitatively estimate visibility, we included a visibility factor as a random effect in all GAMMs. To further account for the influence of local visibility on survey observations, we took a conservative approach and modeled probability of encounter instead of variation in abundance, as variation in abundance is more sensitive to the influence of local visibility. Only four of nine environmental and structural variables were found to have a significant effect on fish distributions in the horizontal dimension in this study, and it is probable that some variables that had nuanced, non-significant effects on the distribution patterns of some species may have a significant effect on the abundance of these species (Vaz et al. 2006; Grüss et al. 2014; Weijerman et al. 2019). As another conservative measure, we excluded species that were encountered on <10% of survey events (i.e. rare species) to help ensure that the results were based on sufficient data. Visibility will almost always be an issue with camera surveys of reef-associated fishes in the GOM, but use of alternative technologies, such as acoustic cameras (e.g. ARIS) combined with other hydroacoustic instruments could help reduce its influence further in future studies.

It may be intuitive that some environmental parameters included in GAMMs in the present study are strongly correlated. In particular, in the horizontal dimension, one may expect many environmental parameters such as salinity and temperature to be strongly correlated with seafloor depth. If this was the case, then including both seafloor depth and environmental predictors that are strongly correlated with seafloor depth in horizontal distribution GAMMs would result in statistical models where depth has a confounding effect and introduces some bias in the analysis (Guisan et al. 2002; Dormann et al. 2013). To avoid this issue, as many studies before us (e.g. Grüss et al. 2018a, 2019; Dance and Rooker 2019; Weijerman et al. 2019), we employed a standard

collinearity analysis to exclude those environmental variables that are strongly correlated with others or with eastings and northings from horizontal and vertical distribution GAMMs (Leathwick et al. 2006; Dormann et al. 2013). The collinearity analysis revealed that seafloor depth was not strongly correlated with any of the other environmental variables included in the horizontal distribution dataset or with easting and northings and, therefore, seafloor depth had no confounding effect in horizontal distribution GAMMs. Similarly, in the vertical dimension, one may expect distance from shore to be strongly correlated with seafloor depth. Although we did not include distance from shore in vertical distribution GAMMs, preliminary analyses examining Pearson's correlation coefficients between distance from shore and the environmental variables included in the vertical distribution dataset revealed that seafloor depth and distance from shore were not strongly correlated, which was most likely due to the protrusion of Louisiana compared with other coastal states (Fig. 3.1) and the restriction of the study platforms to <150 m depth. Since these correlations may be study specific, we emphasize the importance for future studies using GAMMs or similar regression approaches to implement standard collinearity analysis prior to fitting regression models to avoid confounding effects and associated biases (Guisan et al. 2002; Dormann et al. 2013).

The spatio-temporal scale of this study (namely a single ocean basin in the summer months, and the exclusion of platforms > 150 m depths located off of the continental shelf) likely had an influence on the results, particularly regarding the effects of temperature in the horizontal dimension, and DO concentration in the horizontal and vertical dimensions. Given prior work on DO concentration's effect on fish distribution in the vertical (Stanley and Wilson 2004; Reeves et al. 2018; Munnelly et al. 2019) and horizontal dimensions (Szedlmayer and Shipp 1994; Craig and Crowder 2005, Craig et al. 2013), we expected DO concentration to be influential for more species than just Red Snapper. However, only 8 out of our 114 surveys were conducted at platforms with hypoxic water layers (i.e. where DO concentration is less than 2.0 mg/L), and 18 out of 502 water layers surveyed had ≤ 50% oxygen saturation (a more biologically-relevant indicator of hypoxia; Munnelly et al. 2019). It is, therefore, possible that areas with low DO concentration were not

sufficiently sampled in this study for effects on the vertical or horizontal distribution of some species to be apparent. Additionally, the range of temperatures included in the horizontal distribution dataset (21.48 – 30.58°C) was relatively narrow due to the aforementioned spatial and temporal scales at which this study was conducted. Our results show that the high relief of platform habitat allows fishes to shift their vertical distributions to seek thermal optima while remaining structure-associated (Figs. 5-7), and thus, these effects are more likely to manifest in horizontal distribution patterns with more extreme seasonal shifts in temperature, which have previously been suggested to have an influence on platform-associated fish assemblages (Gallaway and Lewbell 1982). This, and the relatively extensive spatial scale of the present study, may account for differences between our results and results from other studies that employed similar methods in platform habitats. Examples of this include the lack of influence of DO concentration, depth and salinity on Red Snapper distribution in the horizontal dimension as shown by Munnelly et al. (2019) on platforms in coastal Louisiana (although interactions between parameters and a binary 'hypoxia' variable were significant), and the opposite effect of seafloor depth on Red Snapper as shown by Stanley and Wilson (2000), although direct comparison with Stanley and Wilson (2000) is difficult given that they studied variation in abundance, while we focused on probabilities of encounter in this study.

In future studies, considering that habitat utilization varies with life stage and body size in reef fishes (Anderson et al. 1989; Dahlgren and Eggleston 2000; Powers et al. 2018), it would be advantageous to examine the effects of the suite of parameters included in the present study on the distribution or abundance of specific life stages and sizes to gather a complete picture of potential impacts. For example, Red Snapper are known to associate with platforms after age two, but gradually become less associated with platform habitat as they age (Gallaway et al. 2009 and references therein). So, alterations to the availability of platform habitat would likely have the greatest impact on young adult Red Snapper compared to other life stages.

CONCLUSIONS AND APPLICATIONS

Climate change is affecting species distribution and ecology in a variety of habitats throughout the world (e.g. Walther et al. 2002; Perry et al. 2005). In addition to increasing temperatures, climate change is also expected to alter Mississippi River discharge, which may increase the size and duration of hypoxic areas (Justić et al. 1996). The availability of high relief reef habitat in the GOM is changing as well, with petroleum platforms being removed at a far greater rate than they are being constructed in recent years (BOEM 2019). The results of the present study suggest that these changes are likely to affect some species more than others. Given the effect of temperature on their vertical distributions, it may be expected that rising temperatures would influence the distributions of Atlantic Spadefish, Bermuda Chub, Blue Runner, Greater Amberjack, and Red Snapper more than the other study species. The altered Mississippi River discharge expected with climate change may impact the salinity of the region, and this could be particularly influential for Bermuda Chub, Greater Amberjack, and Red Snapper. Further, results from the present study suggest that Red Snapper would be most impacted by the intensification of the hypoxic 'dead zone' expected as climate change advances. Additionally, the removal of platforms in offshore areas could restrict biogeographic ranges of Bermuda Chub, Greater Amberjack and Vermilion Snapper on platforms, but the resultant lower density of platforms could be favorable for Blue Runner and Crevalle Jack.

Overall, though, we emphasize that the distributions of the majority of the study species were not found to be influenced by the modeled parameters at the ranges they were sampled. Fishes that thrive in dynamic GOM ecosystems are likely to be tolerant to a wide range of environmental conditions, and given the relative scarcity of similar high-relief reef habitat in many areas, these species may tolerate a range of conditions to remain platform-associated. Indeed, the results of the present study support this hypothesis, and multiple studies have suggested strong association with nearshore platforms despite measurable variations in environmental conditions (Reeves et al. 2018; Munnelly et al. 2019). However, it remains to be seen if the species that were seemingly unaffected by environmental parameters will continue to associate with platforms universally

across climate regimes, as past shifts in climate mode have been associated with large changes in ecological processes and fishery landings in the GOM (Karnauskas et al. 2015).

Our findings may be useful for efficiently addressing spatial data gaps, predicting future species distribution shifts, assessing the impacts of disasters, and setting appropriate scales for stock and ecosystem assessments. If projections on how the suite of parameters included in the present study may change over time were available, as well as predictions of how the number of available platforms might be altered, it would be possible to model distribution shifts of the study species on platforms throughout the GOM through the relationships described in the present study. The lack of effect of platform age and complexity suggest that platforms may be filling the same role for the study species, regardless of variation in their specific characteristics. When developing data collection programs to inform assessments, it would, therefore, be more beneficial to examine gradients in platform density (here represented as the number of platforms within five km) and distance from shore than gradients in complexity and age, as has been done in other studies of fishes in reef habitats (Lingo and Szedlmayer 2006; Burt et al. 2011; Granneman and Steele 2015). Environmental and structural drivers of the distribution patterns of some species (Tables 4 and 5 and Figs. 2-7) should be noted, although the lack of influence of the suite of parameters included in the present study on the majority of study species could lead one to reasonably assume that representatives from the full cadre of platform-associated species examined in the present study would likely be present at a given platform across gradients in these parameters. New tools are emerging to aid fisheries management in the context of Mississippi River input related phenomena (e.g. ecosystem simulation models focusing on hypoxia and river diversion issues; de Mutsert et al. 2016; Dynamic Solutions 2016), and ecosystem considerations are going to be increasingly incorporated into the stock assessment process for GOM fishes (Grüss et al. 2017; O'Farrell et al. 2017). In this context, it will be important to recognize platforms as unique areas in which fishes can alter their vertical distribution to avoid water layers containing stressors (e.g. extremes in temperature or DO concentration) that may have extirpated them from other habitats, allowing them to remain structure-associated and retain their horizontal biogeographic distributions. Thus,

when making predictions about future distribution shifts, disaster impacts in specific areas, and conducting stock assessments incorporating ecosystem considerations, the number of available or un-impacted platforms should be among the most important consideration for these fishes.

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Chapter 4: Optic-acoustic analysis of fish communities at petroleum platforms

ABSTRACT

Petroleum platforms provide high-relief reef habitat in several ocean basins and are important to fishes and fishers alike. To determine which variables were important for shaping platform-associated fish communities on a basin-wide scale in the U.S. Gulf of Mexico, we employed optic and acoustic methods to measure fish distribution (geographic and water-column), abundance, biomass, density, size, diversity, and richness at 54 platforms. We found that variables related to freshwater inflow and meso-scale circulation patterns (e.g. salinity) affected more metrics than platform characteristics (e.g. platform depth). Platform fish assemblages varied gradually along gradients of these variables instead of exhibiting distinct community groupings in non-metric multidimensional scaling space. These effects contributed to the presence of biomass, density, diversity, and richness 'hotspots' at platforms offshore of the Atchafalaya River. Our findings underscore the importance of freshwater inflow and circulation patterns in explaining variation in reef fish communities in the U.S. Gulf of Mexico.

INTRODUCTION

Petroleum platforms (hereafter 'platforms') are immensely popular fishing locations in U.S. waters of the Gulf of Mexico (GOM), as they are easily located by fishers and provide a unique form of relief and complexity among reef habitats in the region. Platforms support abundant fish communities, and they allow fishes to redistribute vertically to avoid stressors (e.g. hypoxia, predation) while remaining associated with refugia (Stanley and Wilson 2004; Reeves et al. 2018b; Egerton et al. 2021). However, there have been substantial reductions in the number of platforms in the GOM over the past decade (BOEM 2019; Munnelly et al. 2020). There is debate over whether platforms and similar structures make a substantial contribution to fish stocks (Bohnsack

1989; Claisse et al. 2014; Karnauskas et al. 2017), but platforms certainly have an impact on local ecology and fishing opportunities of coastal communities (Franks 2000; Gallaway et al. 2009; Ajemian et al. 2015). By extension, so do the explosive severance procedures often used to decommission platforms (LGL 2019). Much effort has been devoted at different scales to determining which environmental conditions and platform characteristics affect aspects of platform-associated fish communities, but the dynamic nature of the GOM complicates efforts to draw collective inferences.

Surveying platforms across the GOM comes with a unique suite of challenges, including accommodating the industrial activities that occur on them and substantial variation in platform footprint, water depth, and water clarity. Several approaches have been successfully executed, including active acoustic (Stanley and Wilson 1996, 1997; Egerton et al. 2021), hook-and-line (Stanley and Wilson 1991; Rester et al. 2017), optical surveys by various means (Ajemian et al. 2015; Bolser et al. 2020; Wetz et al. 2020), and various combinations of these (Stanley and Wilson 2000, 2004; Reynolds et al. 2018). Prior work has described depth-specific assemblage zonation (Gallaway and Lewbel 1982; Wilson et al. 2006; Ajemian et al. 2015), and seasonal fluctuations in fish density and community composition (Stanley and Wilson 1997; Barker and Cowan 2018; Reynolds et al. 2018). Further, a variety of environmental and habitat-related influences on platform-associated fishes have been identified, including dissolved oxygen (DO) concentration (Stanley and Wilson 2004; Reeves et al. 2018b; Egerton et al. 2021), salinity (Gallaway and Lewbel 1982; Munnelly et al. 2019; Bolser et al. 2020), temperature (Gallaway and Lewbel 1982; Stanley and Wilson 1997; Reynolds et al. 2018), artificial light (Barker and Cowan 2018), substrate type, river discharge and *Sargassum* abundance (Munnelly et al. 2020), distance from shore (Bolser et al. 2020), and the number of platforms within 5 km (Bolser et al. 2020; Egerton et al.

2021). These studies provide an abundance of valuable information but were conducted at different scales with different methodology. To gain a comprehensive understanding of the relative impact of these factors on a basin-wide scale, it is advantageous to analyze multiple metrics derived from contemporaneously collected data.

Optic-acoustic surveys, which typically pair underwater cameras with split-beam echosounders, efficiently provide data on multiple metrics at different resolutions. This approach has increasingly been applied to study fishes around natural and artificial reefs (Lee 2013; Egerton et al. 2018; Demer et al. 2020). Around platforms, optic-acoustic surveys have been applied to describe patterns of distribution, biomass, and density of fishes at different spatial and temporal scales (Stanley and Wilson 2000, 2004; Soldal et al. 2002) and to describe differences in fish communities between standing and toppled platforms (Reynolds et al. 2018). Optic-acoustic methods are not free of biases, including water clarity for optics, target discrimination and target strength estimation for acoustics (Sawada et al. 1993; Simmonds and MacLennan 2008), and exclusion of crypto-benthic fishes for both methods. Nevertheless, optic-acoustic surveys are a relatively rapid, efficient, and robust approach for characterizing water-column fish communities (Demer et al. 2020).

The present study employs the contemporaneously collected optic and acoustic data of Bolser et al. (2020) and Egerton et al. (2021) to analyze fish communities at platforms and draws collective inferences from these analyses and the published findings of Bolser et al. (2020) and Egerton et al. (2021). We describe our use of optic-acoustic methods to (1) characterize variation in the biomass, size, density, diversity, and richness of water-column fishes at platforms; (2) examine how environmental and platform variables affect fish distribution (water-column and geographic), abundance, biomass, size, density, diversity and richness at platforms in different

ways; (3) estimate the average abundance of water-column fishes at platforms; and (4) investigate the impact of scale (i.e. spatial extent and sample size) on our ability to describe environmental and structural effects on fish geographic distributions.

METHODS

Data Collection

One-hundred-and-fourteen surveys of 54 platforms were conducted from May – August 2017 and 2018. Platforms were selected via stratified random sampling among depth strata *sensu* Gallaway and Lewbell (1982). Fifty-one platforms were surveyed twice (one optic-acoustic and one optics-only) in a single year, and three platforms were surveyed twice in both years (one each of optic-acoustic and optics-only in both years). More details on platform selection and characteristics are reported by Bolser et al. (2020) and Egerton et al. (2021).

A Simrad EK80 split-beam echosounder with a 120 kHz transducer was pole-mounted to the survey vessel and deployed vertically for hydroacoustic surveys. Hydroacoustic data were collected in a spiral pattern around the platform beginning as close as possible to the platform and ending at approximately 100 m away from it. One additional transect on each side of the structure was also conducted. More details on hydroacoustic data acquisition are reported by Egerton et al. (2021).

Following hydroacoustic sampling, the survey vessel was moored to the down-current side of the platform and a YSI EXO sonde was deployed to collect environmental and physical data. The data recorded by the sonde included dissolved oxygen (DO) concentration (mg/L), temperature (°C), and salinity (‰). Seafloor depth (m) and platform characteristics were recorded in the field or measured in QGIS (ver. 3.8.1) using data from the Bureau of Ocean and Energy Management (BOEM 2019), with the exception of the distance to natural hard-bottom habitat. To

calculate the distance to natural hard-bottom habitat, we generated a 0.008º (2 km x 2 km) grid of the presence/absence of rock substrate and reef habitat using data from usSEABED (Buczkowski et al. 2006), ReefBase (http://www.reefbase.org/), and the NOAA Deep Sea Coral Data Portal (https://deepseacoraldata.noaa.gov/). The natural neighbor function in MATLAB (ver. 9.4) was employed to obtain of value of presence/absence of natural hard-bottom bottom habitat for each of the cells of the 0.008° grid. Then, for each of the study platforms, we determined the distance to the nearest natural hard-bottom habitat using the distance function in MATLAB (ver. 9.4). The other platform characteristics included: age (years); number of other platforms within 5 km; distance from shore (km); and number of legs. More details on sonde measurements and platform characteristics are reported by Bolser et al. (2020) and Egerton et al. (2021).

After the sonde sampling, a submersible rotating video (SRV) camera was deployed. The SRV camera was deployed vertically for 6-7 minutes every 10 meters of depth approximately 5-6 meters away from the platform structure (hereafter "standard drops"). A "targeted drop" was conducted in the same manner after hydroacoustic sampling in locations where large schools of fishes were observed on the echosounder. Water clarity was documented for each drop as a visibility score of 1–3 (poor to excellent) assigned by an analyst based on their ability to identify fishes (or platform structures if fishes were not observed) at different apparent distances from the camera. Scoring was qualitative due to the lack of direct distance measurements, but it was still possible to discern if fishes were identifiable at only one distance from the camera (i.e. all members of the same species with the same life stage morphology appeared at the same size on the screen; visibility score of 1), at 2-3 different apparent distances from the camera (visibility score of 2), or more than 3 different distances from the camera (visibility score of 3). More details on SRV camera deployment and visibility scoring were reported by Bolser et al. (2020).

Data Analysis

Hydroacoustic data were processed using Echoview (ver. 8, Echoview Software, Pty.) software. Following similar hydroacoustic studies of platform-associated fishes in the GOM, fish densities were derived through echo integral scaling using *in situ* target strength (*TS*) measurements from single targets (Stanley and Wilson 1997, 2000). Target strength measurements that were compromised by multiple echoes were detected using the Nv and M% indices (Sawada et al. 1993; Simmonds and MacLennan 2008) and were masked in Echoview. Fish densities (per volume) derived in this manner were converted to abundance by multiplying by the volume of water investigated out to 100 m from the platform. Thus, reported fish abundance is within 100 m of the platform structure. Mean *TS* (a proxy for fish size, hereafter referred to as such) and volumetric backscattering (*sv*; a proxy for fish biomass, hereafter referred to as such) were also extracted from hydroacoustic data and were first analyzed along with fish density in Egerton et al. (2021). The findings of Egerton et al. (2021) were analyzed further in the present study to place them in context with other metrics derived from contemporaneously collected data so that collective inferences about platform fish communities may be drawn. More details on hydroacoustic data processing and the caveats associated with *TS* and *sv* being used as proxies for fish size and biomass were reported by Egerton et al. (2021).

Relative abundances of fish species were estimated from SRV camera data at each 10-m depth layer using the MaxN method (Priede et al. 1994), following similar optical studies of platform-associated fishes in the GOM (Barker and Cowan 2018; Reynolds et al. 2018). Counts commenced at each depth layer after the camera settled and analysts observed the platform structure on a 'settled' rotation (typically :30 – :45 s), which typically allowed fishes to resume their normal behavior if it was altered by the camera (Reynolds et al. 2018). When targeted drops were conducted in addition to standard drops, the higher of the two MaxN for a given species was

taken as the MaxN for that depth layer. Hydroacoustic estimates of fish abundance in each 10-m depth layer were apportioned according to the relative abundance (proportion) of each species in each 10-m depth layer. The resultant species abundance at each depth layer was summed across depth layers to provide an estimate of the abundance of each species at each study platform. Cryptic, strongly reef-associated species, and megafauna (Appendix 3) were excluded from the analyses due to either the low likelihood of detection by the echosounder given their extremely close proximity to the platform structure and/or high inconsistency in detection by the SRV camera. Thus, the present study only considered common platform-associated species that were typically found in the water column at distances > ~ 1 m away from the platform structure.

MaxN counts were reduced to encounter/non-encounter at each site to analyze species geographic distribution, species richness and Shannon-Wiener diversity (hereafter 'diversity'; Shannon 1948). For representing data in figures of diversity and richness at sites that were surveyed more than once, a species was recorded as 'encountered' if it was observed in any of the visits and 'not encountered' if it was never observed at the site. Site visits were treated separately in the dataset used to analyze these metrics statistically.

Statistical Analysis

All statistical analyses were conducted in R Studio (ver. 3.6.1). We fit generalized additive mixed models (GAMMs) to examine the influence of environmental conditions and platform characteristics on species richness and diversity. Based on data distribution, we fit Gaussian (for richness) and Quasi-Poisson (for diversity) GAMMs with identity (for richness) and log (for diversity) link functions using the 'mgcv' (ver. 1.8-28) R package. Prior to modelling, correlations between potential predictors were examined, and of the predictors with a correlation coefficient greater than 0.7 in absolute value, the predictor with the lowest mean correlation with diversity

and richness was excluded from the analysis (Grüss et al. 2020). Predictors that were not correlated with one another or with eastings or northings above an absolute value of 0.7 were included as smoothed predictors in the initial models (Grüss et al. 2020). Non-significant predictors were later excluded from the GAMMs, which were re-fit until only significant predictors remained in the final model (Bolser et al. 2020; Egerton et al. 2021). Visibility score, site, and survey team were included as random effects in these models, as water clarity affects fish detectability, sites were visited multiple times, and two survey teams collected data. A tensor term between eastings and northings was also included as a fixed effect to account for spatial autocorrelation in the data. The GAMMs were evaluated using an approach in which Spearman correlation coefficients (Spearman ρ) between GAMM predictions and observed data were calculated and tested to be significantly different from zero (Egerton et al. 2021; Grüss et al. 2021).

We also fit single-predictor negative binomial Generalized Additive Models (GAMs) with a log link function to understand the influence of environmental conditions and platform characteristics on the abundance of three federally-managed platform-associated species: Greater Amberjack (*Seriola dumerili*), Red Snapper (*Lutjanus campechanus*), and Vermilion Snapper (*Rhomboplites aurorubens*). We fit single-predictor GAMs instead of multiple-predictor GAM(M)s to avoid overfitting as the models were fit only to data from platforms with good water clarity (average visibility score > 2.0/3.0; Fig. 1). Models fit to the entire dataset were also explored (see supplementary material). We considered the same predictors in these models as in the GAMMs of species richness and diversity, and the GAMMS fit in Bolser et al. (2020) and Egerton et al. (2021) (excluding turbidity) (Table S4).

In the same manner as the GAMs of abundance, single-predictor binomial GAMs with a logit link function were fit to encounter/non-encounter data of Greater Amberjack, Red Snapper,

and Vermilion Snapper to investigate influences on their geographic distributions at the same scale as the abundance. Predictors included in this analysis were the same as above (Table S4). A similar procedure was used to study the geographic distributions of these species using the full dataset by Bolser et al. (2020), but the analysis in the present study was conducted to investigate the role of scale in our ability to describe the effects of environmental conditions and platform characteristics on fish geographic distributions.

Wisconsin-standardized encounter/non-encounter data for each species were analyzed by non-metric multi-dimensional scaling (NMDS) using Jaccard distances through the 'metaMDS' function in the 'vegan' (ver. 2.5-6) R package to examine variation in assemblage. A smoothed surface for each of the significant predictors in diversity and richness GAMMs was generated in the NMDS space using the 'ordisurf' function in 'vegan' for observation of the interplay between gradients in these variables and variation in assemblage. A smoothed surface for seafloor depth was also generated and plotted given the findings of prior work linking variation in assemblage with seafloor depth (e.g. Gallaway and Lewbel 1982; Wilson et al. 2006; Ajemian et al. 2015). The 'ordisurf' function fits a GAM to generate the smoothed surface. We modified the base settings of 'ordisurf' to fit GAMs with penalized thin plate regression splines (fx = T, bs = "ts"), and generated plots by modifying code from the 'ggordiplots' R package. Species that were significantly associated with the spread of NMDS points (i.e. their encounter/non-encounter was associated with differences in the position of sites in the NMDS space) were identified using the 'envfit' permutation function in 'vegan', and their corresponding vectors were plotted. These vectors represented the directionality and strength of the relationship.

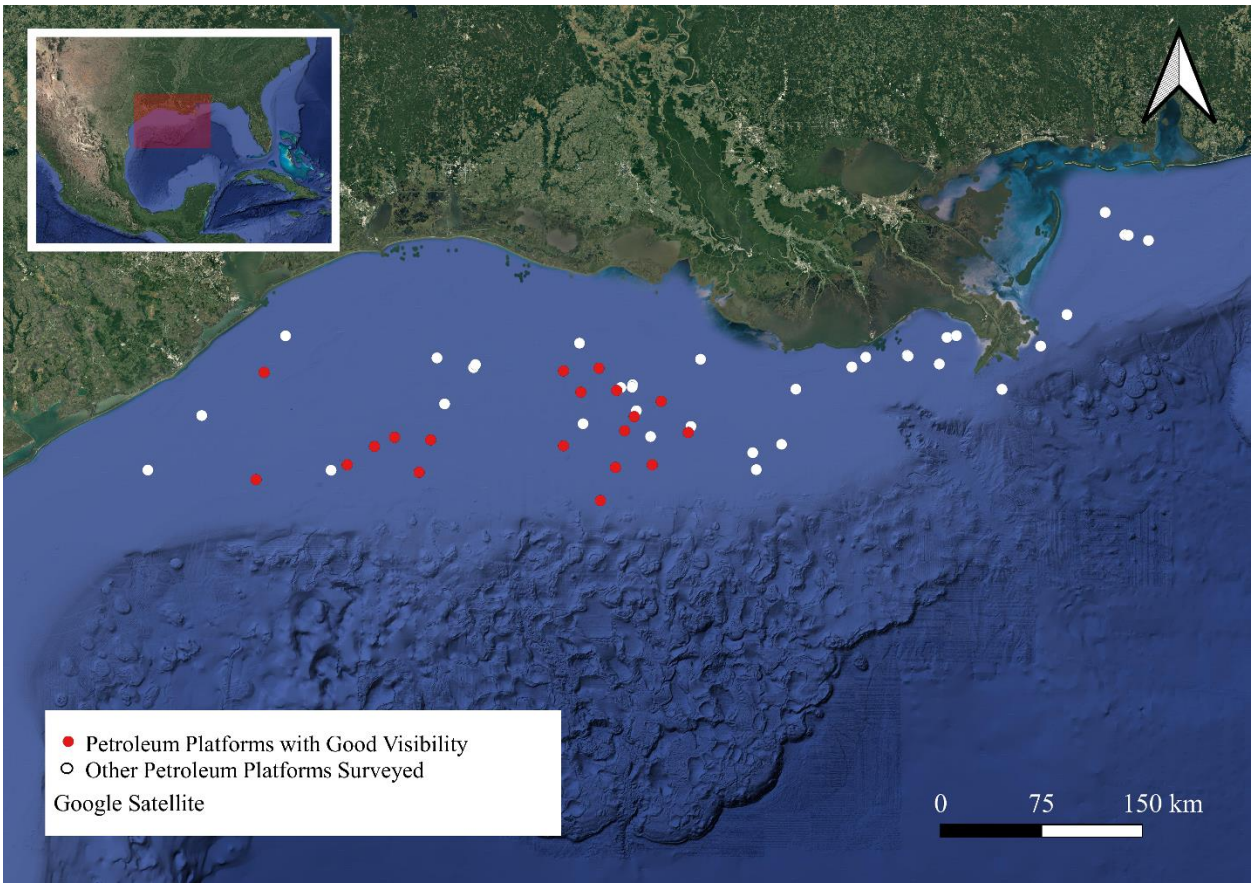

Figure 4.1: Petroleum platforms included in this study. Red dots represent platforms with good water column clarity (average visibility scores > 2.0/3.0), and white dots represent all other platforms included in the study. Map data © Google

RESULTS

Average Abundance of Species

Species abundances were highly variable between sites, as evidenced by standard deviations of abundance, which exceeded mean abundances for every species except Red Snapper (Table 4.1). Percentage differences between abundance estimates from sites with good visibility (average visibility scores > 2.0/3.0, n = 19) and all sites (n = 54) ranged from 19.0 – 350.7% (mean = 65.6%) for the 15 most abundant species in our dataset. Abundance estimates for all are reported in Table S2. Though study platforms were distributed widely from nearshore to far offshore areas

off the coasts of Texas through Alabama, platforms with good water clarity were generally found offshore in the western GOM (Fig. 4.1).

Table 4.1: Average and standard deviation of optic-acoustic abundance within 100 m of platform structure for the 15 most abundant species in our dataset. The average and standard deviation of abundance of fishes is presented for study sites with good water column visibility (average visibility scores > 2.0/3.0, n = 19), and for all study sites (n = 54), along with the percentage difference in abundance estimates derived from these datasets.

Species	Average Abundance from Sites with Visibility Scores > 2.0/3.0 (Standard Deviation)	Average Abundance from All Sites (Standard Deviation)	Percentage Difference in Average Abundance
Atlantic Bumper (*Chloroscombrus chrysurus*)	11,778 (22,662)	4,749 (14,161)	59.68
Blue Runner (*Caranx crysos*)	6,869 (8,750)	8,959 (14,056)	30.44
Bermuda Chub (*Kyphosus sectatrix*)	4,194 (8,839)	1,673 (5,446)	60.10
Red Snapper (*Lutjanus campechanus*)	3,871 (2,971)	2,347 (2,489)	39.37
Greater Amberjack (*Seriola dumerili*)	2,243 (7,308)	1,566 (5,965)	30.21
Crevalle Jack (*Caranx hippos*)	2,121 (6,831)	1,484 (5,702)	30.03

Vermilion Snapper (*Rhomboplites aurorubens*)	1,190 (2,169)	964 (3,184)	19.00
Atlantic Moonfish (*Selene setapinnis*)	864 (3,638)	304 (2,121)	64.83
Atlantic Spadefish (*Chaetodipterus faber*)	751 (1,391)	3,383 (16,124)	350.67
Guachanche Barracuda (*Sphyraena guachancho*)	660 (2,330)	224 (1,370)	66.07
Gray Snapper (*Lutjanus griseus*)	655 (1,313)	516 (1,253)	21.24
Horse-Eye Jack (*Caranx latus*)	576 (1,913)	217 (1,130)	62.30
Rainbow Runner (*Elagatis bipinnulata*)	553 (2,296)	270 (1,410)	51.21
Almaco Jack (*Seriola rivoliana*)	289 (688)	383 (1,840)	32.39
Bluefish (*Pomatomus saltatrix*)	192 (837)	65 (488)	66.07

Table 4.1 (continued)

Diversity and Richness

Species diversity and species richness varied spatially, with the lowest richness and diversity found on platforms nearest to the Mississippi River outflow, and the highest generally at offshore platforms in the western GOM (Figs. 4.2 & 4.3). When these results were considered

along with the findings of Egerton et al. (2021) on fish biomass and size proxies (see Egerton et al. 2021 for details) and density from acoustic data collected at the same site visit, we observed that the sites with the highest values of diversity and richness also tended to exhibit high fish biomass and density values (Figs. 4.2 & 4.3).

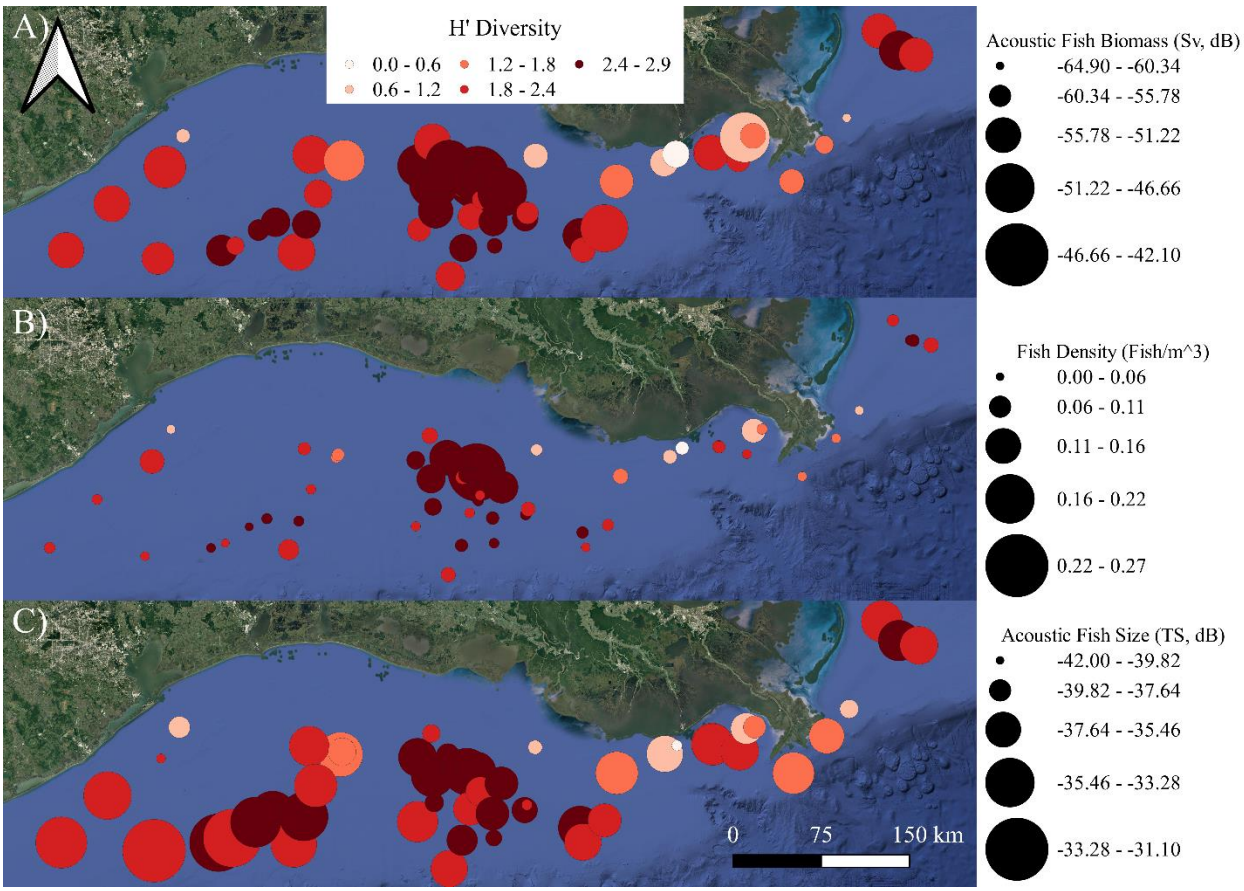

Figure 4.2: Shannon-Wiener diversity (H') of water-column fishes at each site (color) and acoustic measures of A) fish biomass, B) density, and C) size from Egerton et al. (2021). Note that acoustic measures of fish biomass and size are proxies for these metrics (Egerton et al. 2021). Map data © Google.

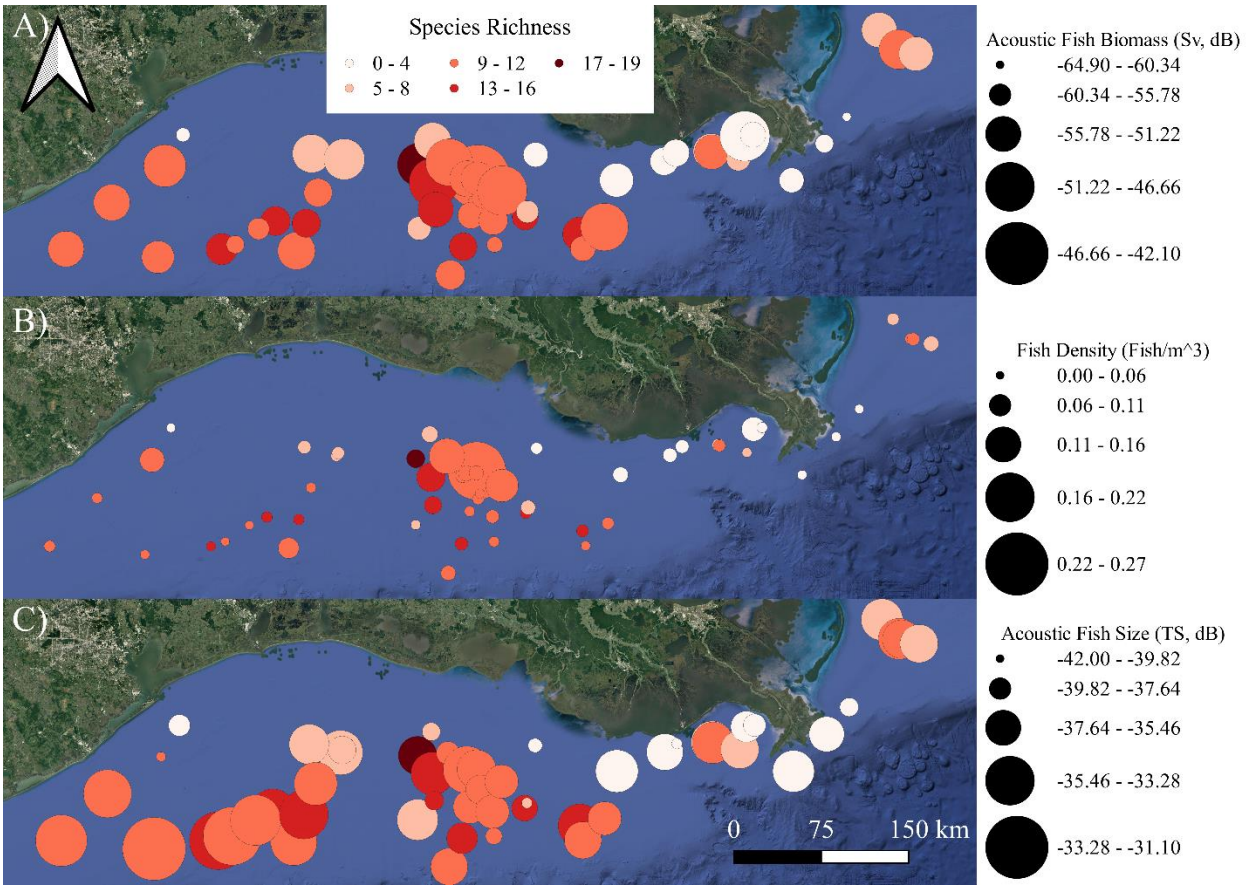

Figure 4.3: Species richness of water-column fishes at each site (color) and acoustic measures of A) fish biomass, B) density, and C) size from Egerton et al. (2020). Note that acoustic measures of fish biomass and size are proxies for these metrics (Egerton et al. 2021). Map data © Google.

The GAMMs fit to species richness and diversity data suggested that salinity and distance from shore explained a large proportion of the variance in diversity (Fig. 4.4) (adjusted-R^2: 0.50, CI: 0.37 - 0.64) and richness (Fig. 4.5) (adjusted-R^2: 0.45, CI: 0.32 - 0.59). There was a positive relationship between diversity and salinity from approximately 26 to 33 ‰, after which the relationship was slightly negative (Fig. 4.4). Similarly, there was a positive relationship between diversity and distance from shore until approximately 90 km from shore, after which the relationship was negative (Fig. 4.5). The effects of salinity and distance from shore on richness showed similar patterns (Fig. 4.5). Distance from shore explained the majority of the variance in

diversity (Fig. 4.4) and species richness (Fig. 4.5) compared to salinity, eastings and northings. The Spearman ρ of the richness GAMM was 0.62 (CI: 0.51 - 0.77, $p < 0.0001$) and the Spearman ρ of the diversity GAMM was 0.70 (CI: 0.61 - 0.84, $p < 0.0001$), so both GAMMs passed the evaluation test and can be employed for statistical inferences. These results, when considered along with the results of Bolser et al. (2020) and Egerton et al. (2021), suggest that variables related to freshwater inflow and meso-scale circulation patterns affect the greatest number of aspects of platform-associated fish communities (Table 4.2).

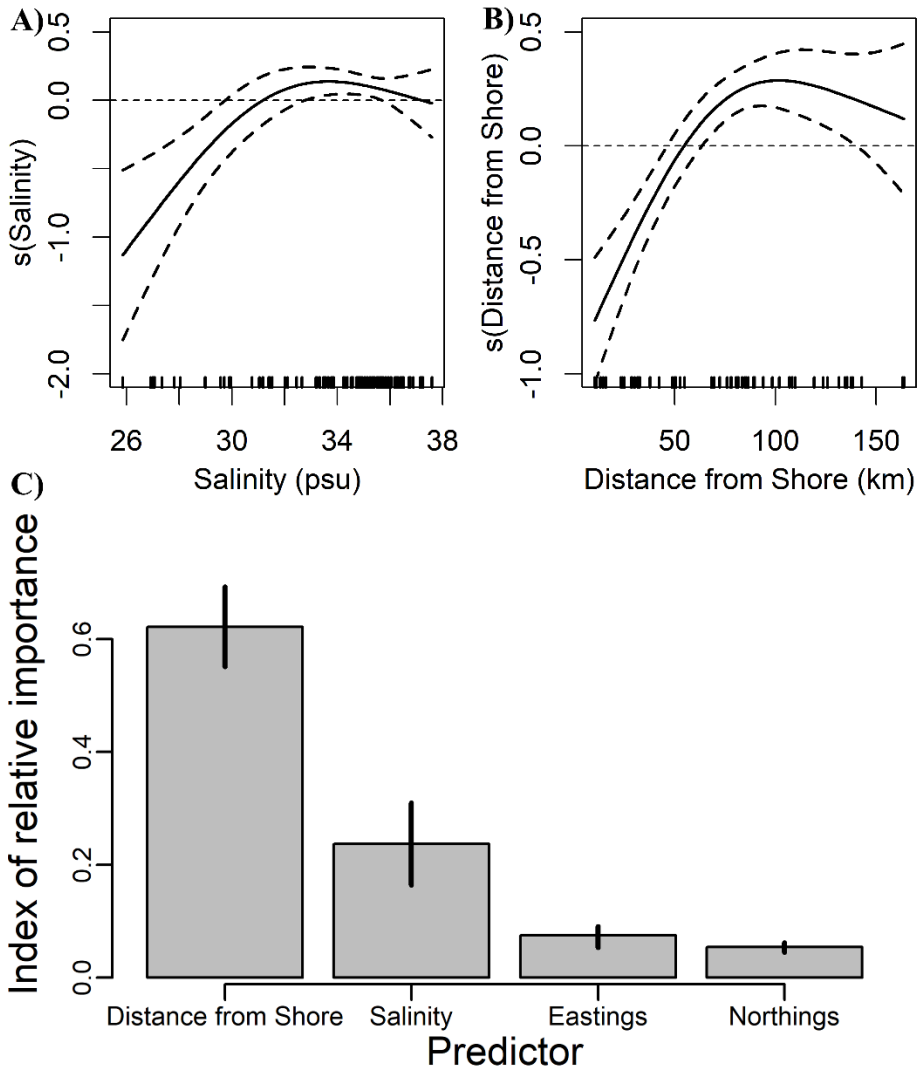

Figure 4.4: Quasi Poisson Generalized Additive Mixed Model (GAMM) results for Shannon-Wiener diversity. A) Marginal effect of salinity on diversity, B) marginal effect of distance from shore on diversity, C) relative importance of predictors in the diversity GAMM.

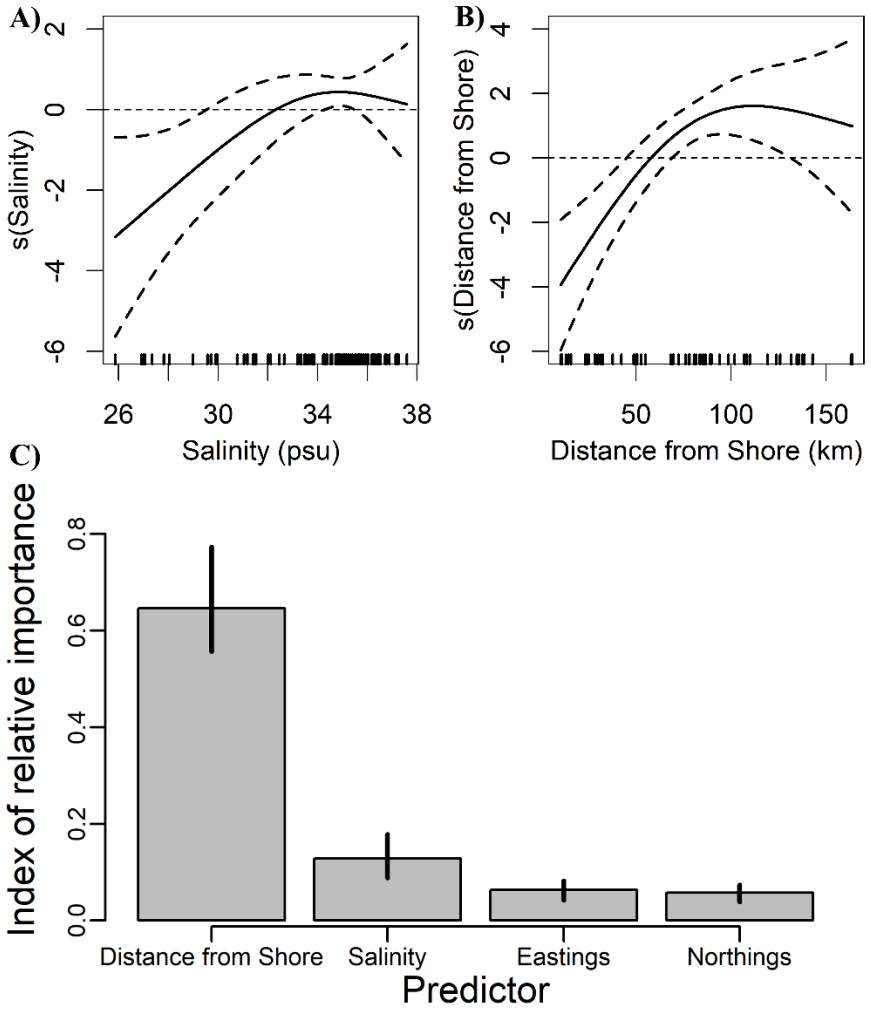

Figure 4.5: Gaussian Generalized Additive Mixed Model (GAMM) results for species richness. A) Marginal effect of salinity on species richness, B) marginal effect of distance from shore on diversity, and C) relative importance of predictors in the species richness GAMM.

Table 4.2: Predictors that significantly influenced optic and acoustic metrics that describe water-column fish communities associated with petroleum platforms in the U.S. Gulf of Mexico. A "+", "-", or "D" indicates that the predictor had a significant positive, negative, or domed relationship with a metric, respectively. A gray box indicates that the predictor was not considered in this type of analysis. The species distribution results come from Bolser et al. (2020) and the fish biomass, density and size results come from Egerton et al. (2021). Note that acoustic measures of fish biomass and size are proxies for the true values of these metrics (Egerton et al. 2021).

Parameter	Species richness (optic)	Shannon-Wiener diversity (optic)	Species distribution – biogeographic (optic)	Species distribution – depth (optic)	Fish biomass (acoustic)	Fish density (acoustic)	Fish size (acoustic)
Salinity (psu)		X	X (2 spp.)	X (2 spp.)	X	X	X
Temperature (C)				X (5 spp.)	X	X	X
Dissolved oxygen Concentration (mg/L)			X (1 spp.)	X (1 spp.)		X	
Distance from shore (km)		X	X (3 spp.)				
Number of platforms w/in 5 km			X (2 spp.)		X		

Seafloor depth (m)	X	X (1 spp.)

Table 4.2 (continued)

Effects on the Distribution and Abundance of Greater Amberjack, Red Snapper, and Vermilion Snapper

The geographic distributions of Greater Amberjack, Red Snapper, and Vermilion Snapper were not influenced by any predictors included in GAMs at the sites with good water clarity (the reduced dataset). Similarly, the abundances of Red Snapper and Vermilion Snapper were not influenced by any of the predictors included in GAMs, while the abundance of Greater Amberjack had a positive relationship with distance from shore ($p < 0.001$; EDF = 1.07; adjusted-$R^2 = 0.26$; Table 4.3, Appendix 3). Differences between the geographic distribution results of the present study and those of Bolser et al. (2020) suggested that spatial scale likely affected our ability to describe the effects variables on geographic distribution and abundance (Table 4.3).

Table 4.3: Summary of significant predictors in models fitted to explain variation in abundance and encounter/non-encounter in the present study and Bolser et al. 2020. The generalized additive mixed models (GAMMs) from Bolser et al. 2020 were fit to data from all platforms displayed in Fig. 1. and included random effects for site, survey team and visibility, as well as a tensor term between eastings and northings to account for spatial autocorrelation. The negative binomial and binomial generalized additive models (GAMs) developed in the present study were only fit to data with good water column visibility (average visibility score > 2.0/3.0; red colored platforms in Fig. 1), and were also fit to data from one site visit by one survey team. A "+", "-", or "D" indicates that the predictor had a significant positive, negative, or domed relationship with a metric, respectively.

Species	Parameter	Negative Binomial GAM (abundance)	Binomial GAM (encounter/non-encounter)	Binomial GAMM (encounter/non-encounter; Bolser et al. 2020)
Greater Amberjack (*Seriola dumerili*)	Distance from Shore (km)	+		D
Red Snapper (*Lutjanus campechanus*)	Dissolved Oxygen Concentration (mg/L)			+
	Salinity (psu)			D
Vermilion Snapper	Distance from Shore (km)			+

(*Rhomboplites aurorubens*)

Table 4.3 (continued)

Non-Metric Multidimensional Scaling Analysis of Assemblage

Distinct community groupings were not observed in the NMDS space (Fig. 4.6). Instead, platform fish assemblages varied gradually along gradients of distance from shore, salinity, and depth (Fig. 4.6). Variation in assemblage was associated with the encounter/non-encounter of the following species: Almaco Jack (*Seriola rivoliana*; $p = 0.001$, $R^2 = 0.38$), Atlantic Bumper (*Chloroscombrus chrysurus*; $p = 0.001$, $R^2 = 0.36$), Atlantic Spadefish (*Chaetodipterus faber*; $p = 0.001$, $R^2 = 0.34$), Bermuda Chub (*Kyphosus sectatrix*; $p = 0.001$, $R^2 = 0.55$), Cobia (*Rachycentron canadum*; $p = 0.001$, $R^2 = 0.21$), Crevalle Jack (*Caranx hippos*; $p = 0.001$, $R^2 = 0.30$), Gray Triggerfish (*Balistes capriscus*; $p = 0.33$, $R^2 = 0.12$), Great Barracuda (*Sphyraena barracuda*; $p = 0.001$, $R^2 = 0.50$), Greater Amberjack ($p = 0.001$, $R^2 = 0.56$), Ocean Triggerfish (*Canthidermis sufflamen*; $p = 0.003$, $R^2 = 0.23$), Rainbow Runner (*Elagatis bipinnulata*; $p = 0.01$, $R^2 = 0.15$), Red Snapper ($p = 0.002$, $R^2 = 0.28$), Sheepshead (*Archosargus probatocephalus*; $p = 0.005$, $R^2 = 0.20$), and Vermilion Snapper ($p = 0.003$, $R^2 = 0.20$) (Fig. 4.6).

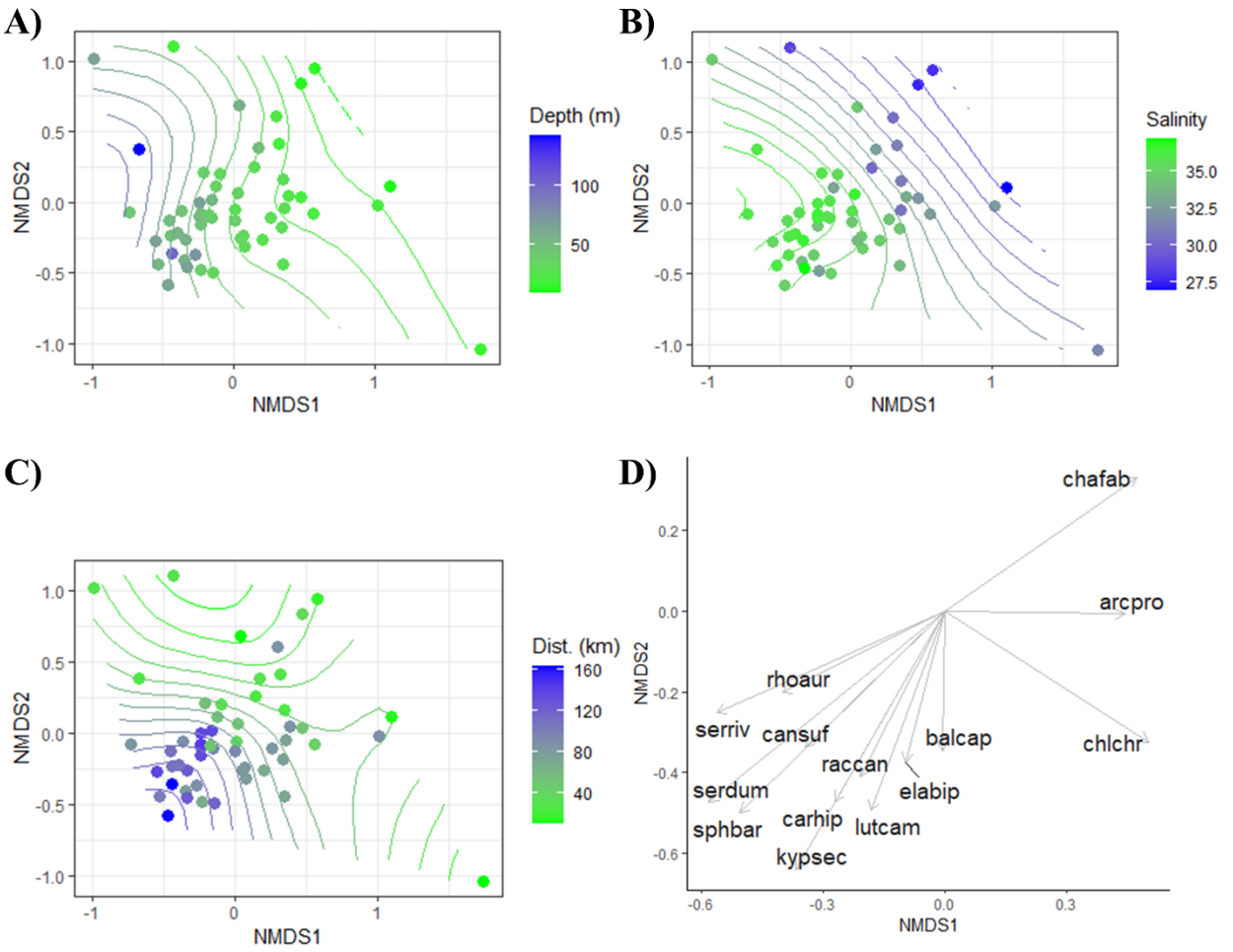

Figure 4.6: Non-metric multidimensional scaling plot of fish assemblage (encounter-non/encounter) and smoothed contours of A) seafloor depth, B) salinity, and C) distance from shore. Points represent fish assemblage at each site and are colored by the measured values of A) seafloor depth, B) salinity, and C) distance from shore to display how measured values relate to smoothed contours of those variables. Species codes and vectors are displayed in panel D) for those fish species that were significantly associated with the spread of points and were, therefore, characterized variation in assemblage. Note that panel D has a different scale than A-C to so that species codes and vectors may be viewed clearly. Species codes: arcpro = Sheepshead (*Archosargus probatocephalus*), balcap = Gray Triggerfish (*Balistes capriscus*), cansuf = Ocean Triggerfish (*Canthidermis sufflamen*), carcry = Blue Runner (*Caranx crysos*), chafab = Atlantic Spadefish (*Chaetodipterus faber*), chlchr = Atlantic Bumper (*Chloroscombrus chrysurus*), elabip = Rainbow Runner (*Elagatis bipinnulata*), kypsec = Bermuda Chub (*Kyphosus sectatrix*), lutcam = Red Snapper (*Lutjanus campechanus*), raccan = Cobia (*Rachycentron canadum*), serdum = Greater Amberjack (*Seriola dumerili*), serriv = Almaco Jack (*Seriola rivoliana*), sphbar = Great Barracuda (*Sphyraena barracuda*), rhoaur = Vermilion Snapper (*Rhomboplites aurorubens*).

DISCUSSION

Our analysis of contemporaneously collected optic and acoustic data allowed us to explore the effects of environmental conditions and platform characteristics on many different aspects of platform-associated fish communities. Numerous species may be encountered across a relatively wide range of conditions at platforms (Bolser et al. 2020), but environmental conditions and platform characteristics affected fish community metrics nonetheless. Environmental conditions related to freshwater inflow and meso-scale circulation patterns (e.g. salinity, temperature, dissolved oxygen concentration) affected more metrics than platform characteristics (e.g. distance from shore, number of platforms within 5 km, seafloor depth) (Table 4.2). However, gradual variation in assemblage was observed along gradients of both types of variables in the NMDS space (Fig. 4.6).

The gradients in salinity, temperature, and dissolved oxygen – the variables that affected the highest numbers of our metrics – observed in this study mostly can be attributed to freshwater inflow from the Mississippi and Atchafalaya Rivers and Loop Current-driven circulation patterns. Accordingly, our findings add to existing knowledge of how these meso-scale features affect ecosystem and community dynamics in the GOM (Table 4.2; e.g. Gallaway 1981; Dagg and Breed 2003; Hetland and DiMarco 2008). The effects of salinity, which influenced all of our metrics, on platform-associated fish communities are likely indirect. In other words, it is unlikely that the range of salinities we encountered was physiologically stressful to the fishes in our study. Instead, salinity is negatively associated with productivity (Kim et al. 2020) and tracks Caribbean water masses containing diverse groups of fish larvae in offshore areas of the GOM (Gallaway 1981; Gallaway and Lewbell 1982). Temperature is likely similar to salinity in acting indirectly and tracing water masses (Mamayev 2010). Thus, the effects of salinity and temperature on platform-

associated fishes likely reflect the proximate effect of productivity and other aspects of water masses (e.g. larval transport).

Platform characteristics affected fewer metrics than environmental conditions, but still influenced species richness, diversity, and the distributions of a small number of species (Table 4.2; Bolser et al. 2020). While distance from shore and the number of platforms near the study platform had not been examined explicitly by other authors in other studies of platform fish communities to our knowledge, prior work suggested that assemblages varied by seafloor depth at platforms (Gallaway and Lewbel 1982; Wilson et al. 2006; Ajemian et al. 2015). Patterns observed in the NMDS space (Fig. 4.6) generally support these findings, although seafloor depth was not a significant predictor in any models of community metrics or species geographic distributions (Table 4.2; Bolser et al. 2020), and we did not observe distinct community groupings (Fig. 4.6). Seafloor depth has been useful for designating sampling strata in past studies of platform-associated fish communities, but our results suggest that researchers should also consider distance from shore when planning their sampling schemes.

We found that species richness and diversity often increased with increasing distance from shore (Figs. 4.2-5). Conditions at offshore areas are generally thought to be more stable than at nearshore areas, which likely facilitates the colonization and persistence of corals and small reef fishes that are transported to platforms by meso-scale circulation patterns (Gallaway 1981; Kolian et al. 2017; Kolian and Sammarco 2019). These types of organisms were not considered in the present study, but their presence at offshore platforms may have affected water-column fishes and contributed to the trends we described indirectly. Diverse fish communities also exist at natural hard-bottom habitats in offshore areas, and it is likely that some species observed at platforms interact with nearby natural habitats (Cowan and Rose 2016). However, we did not find that the

distance to natural hard-bottom habitat had an influence on the richness or diversity of water-column fish communities at platforms. In addition to stable conditions and favorable circulation patterns, the lower fishing pressure that offshore platforms likely experience (compared to nearshore platforms) could have also contributed to higher richness and diversity in this area, and at platforms further from shore in general (Pauly et al. 2002) (Figs. 4.2-5).

The most species-rich and diverse platforms tended to have the greatest fish biomasses and densities (Figs. 4.2 & 4.3). This result agrees with prior work which documented a positive relationship between abundance and richness in reef habitats globally (Edgar et al. 2017), but occurs despite opposing effects of salinity on richness and diversity (positive) and fish biomass and density (negative) (Table 4.2). As identified above, salinity and productivity are closely related in the Gulf of Mexico (Kim et al. 2020), and many of the platforms that exhibited high levels of fish biomass, density, diversity, and richness were located offshore of the Atchafalaya River. The Atchafalaya River has an important influence on the productivity and physiochemical characteristics of the region's waters (Hetland and DiMarco 2008; DiMarco et al. 2010; Kim et al. 2020). The fish communities at platforms in this 'hotspot' may be close enough to the Atchafalaya River outflow to benefit from freshwater inflow-derived productivity, yet may be far enough offshore that local effects of hypoxia are not substantial. Freshwater inflow-derived productivity may outweigh local effects of hypoxia in the wider region (de Mutsert et al. 2016), but potentially not at the platforms nearest to the outlet of the Mississippi River, which we observed to have low fish biomass, density, diversity, and richness (Figs. 4.2 & 4.3). These platforms may also fall within a "Brown Zone" where high sediment loading stifles primary productivity (Rowe and Chapman 2002; Kim et al. 2020). In general, however, the comparatively higher primary productivity at nearshore platforms supports more productive fouling communities, which in turn

may support a variety of grazing species (e.g. Sheepshead, Gray Triggerfish, Black Drum *Pogonias cromis*; Reeves et al. 2018a). Despite this, the conditions at offshore platforms appear to support more diverse, rich, and abundant water-column fish communities.

Importantly, platforms further from shore tended to have the best water clarity. Prior research found that water clarity and associated variables (e.g. turbidity) are important drivers of variation in different aspects of fish communities (e.g. Cyrus and Blaber 1992). However, we did not include water clarity as a fixed environmental covariate having a direct effect on the dependent variable in our models, but rather as a random nuisance factor (visibility score) to account for the ability of water clarity to affect species detection with optical methods. Non-optical methods are best suited for documenting the direct effects of water clarity and associated variables on dependent variables, and the acoustic study of Egerton et al. (2021) at our study platforms indicated that turbidity did not affect platform fish communities at a wide spatial scale. Still, water clarity could affect the distribution and abundance of certain platform-associated species, and this should be investigated in future non-optical studies.

Relative abundance measured by optics is more sensitive to water clarity than the encounter/non-encounter data upon which our analyses of distribution, diversity and richness were based. While small numbers of a species that typically avoids the camera may be observed over the course of a survey, relative abundance estimates will be biased towards species that tend to be closer to the camera in low visibility conditions, and this bias is exacerbated when scaling optic relative abundance to acoustic absolute abundance. As such, we presented two sets of estimates of average optic-acoustic abundance: one from sites with good water clarity (the reduced dataset), and one from the full dataset (Table 4.1). We have greater confidence in estimates from the reduced dataset.

Another potential source of bias to consider when interpreting our findings is that data from drop-cameras at different depth layers may not be independent (i.e. it is possible that fishes follow cameras down in the water-column and are counted more than once). Fishes were not observed to follow the camera down on a consistent basis, but occasionally an individual or small group (< 5 individuals) of fish (typically Barracuda, Greater Amberjack, or Almaco Jack) would swim closely to the camera during the transition to a new depth layer. The MaxN method of determining relative abundance that we employed was specifically developed to reduce the incidence and impact of double-counting fishes (Priede et al. 1994), and our exclusion of the first :30 - :45 s of video at each depth layer typically allowed any fishes that followed the camera to resume their normal behavior (Reynolds et al. 2018). However, it was not possible to completely ensure that all fish observations were unique.

In both the full and reduced datatsets, relatively small pelagic planktivores (e.g. Atlantic Bumper, Blue Runner) dominated the platform-associated fish assemblage, followed by larger piscivorous species such as Red Snapper and Greater Amberjack (Table 4.1). Abundances were highly variable for all species (Table 4.1), though in different ways. Species such as Red Snapper and Blue Runner were encountered at most study platforms (Bolser et al. 2020; Appendix 3) but with varying abundances. Others, like Atlantic Bumper or Vermilion Snapper, were encountered at a small number of platforms (Bolser et al. 2020; Appendix 3), but were highly-abundant when they were encountered. Still others such as the Great Barracuda and Gray Snapper were encountered often (Bolser et al. 2020; Appendix 3), but at consistently lower numbers than many other common species.

It was not possible to develop models of species abundance for the full dataset that we were confident about, and the reduced dataset containing only sites with good water clarity covered a

spatial scale that was likely too small to identify variables that affect species abundance. The influence of spatial scale on our ability to describe effects was illustrated by the comparison of geographic distribution analyses between the present study, which employed the reduced dataset, and the study of Bolser et al. (2020), which employed the full dataset. We did not detect any effect of environmental conditions or platform characteristics on the geographic distributions of Red Snapper, Vermilion Snapper, and Greater Amberjack, which differed from the findings of Bolser et al. (2020) (Table 3). Since Bolser et al. (2020) accounted for water clarity in their models, the differences between the study of Bolser et al. (2020) and the present study may be explained by spatial scale. Our examination of the abundance of those species in the reduced dataset solely identified the influence of distance from shore on Greater Amberjack abundance, and based on our comparison of geographic distribution analyses, we conclude that our results were impacted by the restricted spatial scale of the reduced dataset (Table 4.3). Our findings illustrate the problem of extending the conclusions of smaller-scale studies to wide areas (Levin 1992). Scale-dependence of effects and ability to detect them likely explain a large number of the discrepancies in the literature regarding the effects of different variables on platform-associated fishes in the GOM.

The substantial variation in abundance observed for common platform-associated species is more likely explained by variable movement patterns and complex ecological dynamics than simple variation in platform characteristics and environmental conditions at the spatial scale of the reduced dataset (Kraft et al. 2015). For example, while some platform-associated species exhibit homing behavior and relatively high residency on platforms (e.g. Red Snapper, Gallaway et al. 2009; Blue Runner, Brown et al. 2010), they may also travel long distances and spend long periods of time away from the sites at which they were tagged (e.g. Red Snapper, Gallaway et al. 2009). Other species simply associate with platforms opportunistically (Franks 2000). Considering the

behavior of mobile species and the highly variable abundances we observed, and that relatively few species' distributions were influenced by environmental conditions and platform characteristics (Bolser et al. 2020), we conclude that observing a large number of a given species during one visit to a platform does not guarantee the same thing during another visit. This is important to consider when interpreting our results, as despite repeated visits to each site, our sampling was closer to a 'snapshot' than a continuous record of variation of fish communities at platforms. Definitively uncovering the sources of variation in fish abundance at platforms on a basin-wide scale will require relatively long-term observations at platforms.

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Chapter 5: Assessing fish community size spectra with hydroacoustics: Examining the challenges of abundant schools, diverse assemblages, and variable orientations

ABSTRACT

Conducting acoustic studies of fish community size spectra may be challenging when communities are diverse, schooling and swim bladder-less fishes are common, and fish orientation is variable, as is observed in rugose marine habitats. To address these challenges, we conducted 51 optic-acoustic surveys at petroleum platforms throughout the U.S. Gulf of Mexico and estimated fish community size spectra. Acoustically-derived lengths and size spectra slopes were significantly lower than in non-acoustic datasets when *in situ* target strength (*TS* re. dB 1 m) distributions were used to scale the volumetric backscatter (*Sv* re. dB 1 m) of schools to estimate fish density. However, acoustic slopes were comparable to non-acoustic slopes when simulated *TS* values (based on species composition) were used to scale school *Sv*. Orientation did not affect *TS* or slope in our dataset as a whole but may be important for explaining why *in situ* *TS* was unsuitable for scaling school *Sv*. Despite promising comparisons with non-acoustic data, more research is needed before acoustic size spectra slopes can be meaningfully interpreted in rugose marine habitats.

INTRODUCTION

Communities of aquatic organisms are typically structured as pyramids in which many small individuals support fewer larger individuals, and the relationship between abundance and size may be described by a power law relationship (Elton 1946; Sprules and Barth 2015; Edwards et al. 2017). These abundance pyramids – and the inverted pyramids describing biomass distribution – may be represented as size spectra, which are often quantitatively assessed by regressing logged abundance or biomass against logged bins of length or biomass (Trebilco et

al. 2013; Sprules and Barth 2015; Edwards et al. 2017). Size spectra slopes can also be estimated by fitting a probability density function to size distribution data to remove biases associated with binning (Edwards et al. 2017). One of the most informative metrics coming from this type of analysis is the slope of the regression line or distribution, which describes how the abundance or biomass of small organisms compares to the abundance or biomass of large organisms (Bianchi et al. 2000; Daan et al. 2005; Sweeting et al. 2009).

The size spectrum of a community reflects energy flow between trophic levels and the ecological processes that shape it (Trebilco et al. 2013; Sprules and Barth 2015). As such, the size spectra concept has been used to understand food web structure, macroecology, and the influence of environmental stressors or anthropogenic activities on communities (Wilson et al. 2010; Blanchard et al. 2017; Heneghan et al. 2019). For example, fishing preferentially removes larger individuals and species (Mason 1998; Jennings and Kaiser 1998; Berkeley et al. 2004), resulting in steepening (i.e. more negative) size spectra slopes over time and increasing fishing activity (Pope and Knights 1982; Blanchard et al. 2009; Robinson et al. 2017). The size spectra of fish communities may also reveal differences in ecosystem productivity, with communities in areas of high productivity exhibiting steep size spectra slopes due to a high relative abundance of small, planktivorous fishes (Emmrich et al. 2011; Secor 2015). Since size is thought to be the primary determinant of many biological processes in marine organisms (Andersen et al. 2015), size-based community metrics, such as the slope of the size spectrum, are attractive for application in Ecosystem-Based Fisheries Management (Jennings and Dulvy 2005; Shin et al. 2005).

Due to its non-invasive nature and limited selectivity compared to other methods, split-beam hydroacoustics (hereafter ‘acoustics’) represents a promising tool for rapidly collecting the

data necessary to assess size spectra in aquatic environments (Trenkel et al. 2011). Acoustics has been applied successfully to assess fish size spectra in freshwater systems (e.g. Yurista et al. 2014; Wheeland and Rose 2015; de Kerckhove et al. 2015), although the results of validation studies that compared acoustically-derived size spectra with size spectra estimated with other gears have been inconsistent (Coll et al. 2007; de Kerckhove et al. 2015; Daigle 2017). Acoustic technology is not commonly applied to assess size spectra in marine environments, as doing so involves dealing with significant assumptions and uncertainties related to the diverse assemblages and behaviors of marine fishes (Egerton 2017).

The greatest challenge in assessing fish size spectra with acoustics is relating target strength (*TS*, dB re. 1 m; the intensity of the echo returned from an individual fish) to fish length (Simmonds and MacLennan 2008). Acoustic size spectra studies typically employ an empirically-derived general *TS*-length relationship across species (e.g. Yurista et al. 2014; Wheeland and Rose 2015; de Kerckhove et al. 2015). However, converting *TS* to length is most accurate when a specific model is developed for each species of fish observed, as fish swim bladder morphology (or lack of swim bladder) greatly influences *TS* (Foote 1980; McClatchie et al. 1996a; Simmonds and MacLennan 2008). Specific models do not exist for many common species in marine environments, and though applying species-specific TS-length relationships to different taxa is generally not advisable (Foote 1979; McClatchie et al. 1996a), some species within some families may exhibit similar scattering properties (e.g. Benoit-Bird et al. 2003; Boswell et al. 2020). Even so, the intermingling between bladdered and bladder-less fishes that is often observed in marine environments complicates the application of *TS*-length models, as *TS* distributions may overlap between small bladdered fishes and larger bladder-less fishes.

Relating *TS* to length is further complicated by the effect of fish orientation relative to the transducer on *TS.* Since fishes with varying orientations relative to the transducer present different cross-sections of their swim bladder (or body for bladder-less fishes), the measured *TS* of a fish can vary significantly (Nakken and Olsen 1977; McClatchie et al. 1996b; Simmonds and MacLennan 2008). It is possible to collect data on the orientation of fishes by acoustically tracking them through successive pings, but incorporating the effect of orientation in *TS*-length models can be challenging. While there are few *TS*-length models that account for orientation (e.g. Kubečka 1994; Lilja et al. 2000; Johnson et al. 2019), the influence of fish orientation on size spectra metrics can be investigated through simulations (de Kerckhove et al. 2015) and statistical comparisons.

The presence of schooling fishes also affects the ability of acoustic technologies to describe the size spectra of fish communities. In most fish schools, it is not possible to isolate valid single targets or tracked fish. Accordingly, the *TS* of individual fish cannot be measured, and assumptions must be made in order to estimate the *TS* distribution and number of fish within schools. In other applications for acoustic technology (e.g. biomass and abundance estimation), biological ground-truthing data are used to inform the *TS* distribution of fish within schools and generate estimates of fish abundance (Simmonds and MacLennan 2008). Often ground-truthing data are collected by trawling (e.g. de Blois 2020), but this approach is not possible in all habitat types. Another approach is to use *in situ TS* measurements to represent the mean or distribution of *TS* within a school for scaling school volumetric backscatter (*Sv*, dB re. 1 m) to fish density and abundance (e.g. MacLennan 1990; Boswell et al. 2010; Egerton et al. 2021). However, it is not possible to test if the *TS* of surrounding single targets is representative of the *TS* of fish

within schools with acoustic data alone. At present, the degree to which specifying the *TS* distribution of schools in different ways affects acoustic size spectra estimates is unknown.

Many non-acoustic studies of marine fish size spectra are conducted in rugose habitats where schooling and bladder-less fishes may be common (e.g. Graham et al. 2005; Wilson et al. 2010; Robinson et al. 2017). To assess the use of acoustics to estimate size spectra in this kind of habitat, we (1) compared size spectra slopes and fish lengths between acoustic and non-acoustic datasets; (2) examined the impact of using general or species-specific *TS*-length models on size spectra slopes and fish lengths; (3); compared using *in situ TS* distributions with expected *TS* distributions for scaling the echo integral of schools of fish; and (4) quantified the effect of tracked fish orientation on *TS* and size spectra slopes.

METHODS

Study Area and Data Collection

This study focused on fish communities at 48 petroleum platforms throughout the U.S. GOM and took place over a period of 2 years (May through August of 2017 and 2018). Forty-five of the platforms were surveyed once in a single year, and 3 of the platforms were surveyed twice (once in each year). These platforms were selected via random sampling among depth strata *sensu* Gallaway and Lewbel (1982). The study area and data collection procedures are described in greater detail by Bolser et al. (2020, 2021) and Egerton et al. (2021)

A Simrad EK80 split beam echosounder with a 120 kHz transducer (circular beam width of 6.8º; pulse duration = 0.128 ms; specified ping rate = “max”) was employed for acoustic surveys. The echosounder was calibrated using a tungsten carbide sphere according to standard methods prior to each survey event (Demer et al. 2015). The transducer was deployed at a depth

of 1 m using a customized mount on the starboard side of the survey vessel and aimed directly downwards. The survey track followed a spiral pattern beginning as close to the platform as possible (typically ~ 3 m from the legs) and ending approximately 100 m from the platform structure (Egerton et al. 2021; Bolser et al. 2021). 'Passes' were separated by approximately 20 m and an additional transect was conducted perpendicular to the spiral transects on each side of the platform structure (see Figure 2 in Egerton et al. 2021).

To collect data on the identity and relative abundance of fish species, a self-rotating video (SRV) drop-camera was deployed on the down-current side of the platform at 10-m depth intervals for 6–7 min each, and at one additional location within 100 m of the study platform in the same manner if a large school of fish was observed on the echosounder to include transient schools of pelagic fish that were recorded by the echosounder. More details on camera sampling were reported by Bolser et al. (2020, 2021).

Generation of Reference Datasets

To validate acoustic size spectra, it is necessary to compare them with the size spectra estimated with other methods. In rugose marine habitats such as the petroleum platforms we sampled, logistical constraints and gear biases (e.g. selectivity of hook-and-line sampling, visibility and diver avoidance for stereo video, impracticality of trawling around and over structure) limit the techniques that researchers can use to assess size spectra. Ideally, one would ensure an unbiased representation of community size structure by capturing and measuring each individual in the community, or by collecting all individuals after a complete mortality event. While this was not possible at our study sites, Gitschlag et al. (2001) censused fish communities after explosive decommissioning procedures at six petroleum platforms in the GOM. These procedures are typically lethal for nearly all fishes within an approximately 100 m radius of the

platform (Gitschlag et al. 2001; LGL 2019). Since fishes were collected immediately after detonation using multiple surface and underwater gears, we assume that those fish collections accurately represented the fish communities at those decommissioned platforms. We used the data of Gitschlag et al. (2001) (hereafter referred to as 'community census' data, available: https://catalog.data.gov/dataset/fish-mortalities-from-explosive-removal-of-petroleum-platforms-in-the-gulf-of-mexico-1993-to-1999) to estimate fish community size spectra at each of their study sites as a reference that our acoustically-derived size spectra could be compared with. We acknowledge that it is possible that the structure of fish communities at platforms may have changed since the community census data were collected, but believe it to be the best available census of platform fish communities.

In addition to the community census data, we generated an 'expected' size distribution for comparison with our acoustically-derived size spectra at each of our study sites. This expected size distribution dataset consisted of simulated communities at each site based on absolute abundance of fishes derived from the acoustic data, relative abundance of species from SRV camera data, and published biological data for each species (community census, Gitschlag et al. 2001; FishBase, Froese and Pauly 2020). For species documented in the community census, we extracted the mean, standard deviation, minimum, and maximum of total length in the dataset. For species that were not recorded in the community census but were observed in SRV camera surveys, the 'common length', 'length at maturity', and 'maximum length' were extracted from FishBase. The total number of fishes surveyed by the echosounder was multiplied by the proportional abundance of each species from SRV camera data to obtain the abundance of each species. Then, lengths were assigned to each fish of each species by randomly sampling from a truncated normal distribution. The distribution for each species was truncated by a lower

value of either the smallest fish of that species in the community census or the length at maturity from FishBase, and an upper value of the largest fish of that species in the community census or maximum length from FishBase. The distribution was centered around either the mean length of that species in the community census or the common length from FishBase. The standard deviation of the distribution was set to the standard deviation of the length of that species from the community census, or one half of the difference between length at maturity and maximum length from FishBase. Distributions were generated using package 'truncnorm', ver. 1.0-8, in R Studio (ver. 3.6.1). Data for some of these parameters were not available for some species from either data source, and the alternative data used are described in the supplementary material. These datasets were subsequently combined for all species observed in each survey to form a complete water-column fish community, and size spectra slopes were estimated as described below.

Acoustic Data Processing

Acoustic data were processed using Echoview software (version 10; Echoview Software Pty.) following standard procedures (Parker-Stetter 2009). The first 1-3 m of the water column (depending on sea state) were removed to account for the near-field effect of the transducer and to exclude bubbles caused by wave action (Simmonds and MacLennan 2008). Similarly, a 1-m exclusion zone was applied above the seafloor to account for the hydroacoustic dead zone near the seabed (Ona and Mitson 1996). Echograms were scrutinized to remove bubbles that penetrated deeper into the water column, electronic noise, and the platform structure. Background noise was removed using the Echoview background removal operator with a maximum noise value of 125 dB and minimum signal to noise ratio of 10 dB. TS data were thresholded at -55 dB, and Sv data were thresholded at -61 dB TSu (uncompensated target

strength) following Parker-Stetter (2009) to account for off-axis detections. These thresholds were chosen to exclude most planktonic scattering sources and include most fishes, but it should be acknowledged that large plankton and invertebrates may not have been completely excluded.

To generate a complete representation of the fish community sampled acoustically, this analysis included tracked fishes and schools of fishes. A fish tracking algorithm was employed within Echoview with parameters set to their defaults, and the mean TS across detections was used to define the TS of each tracked fish. Similarly, the school detection algorithm within Echoview was used to detect and delineate school shapes within the echogram with minimum total school height, minimum candidate length, minimum candidate height, and minimum total school length set to 3 m, maximum vertical linking distance set to 5 m, and maximum horizontal linking distance set to 20 m. These parameters were chosen after preliminary examination of computing performance and school detection success. Final school detections were verified by an analyst.

We tested four different scenarios for relating school *Sv* to the abundance of fishes within schools. In the first, we scaled the *Sv* of schools by the *in situ TS* distribution of single targets (pulse length determination level of 6 dB, minimum normalized pulse length of 0.7 seconds, maximum standard deviation of 0.6 degrees for major and minor-axis angles) around them (1-3 meters from the school boundary, or the nearest possible values if none existed within that range). This procedure was conducted in the following manner:

$$N = \sum_{n}^{i} \frac{sv}{\sigma bs_i} * (p_i * V)$$

where *N* is the number of fishes in a given school, *sv* is the mean volumetric backscatter of the school in the linear domain, σbs_i is the *TS* of single targets around the school in 3-dB bin *i*

in the linear domain, p_i is the proportion of single target observations around the given school within *TS* bin *i*, and *V* is the volume of the school. The midpoint of each 3-dB bin was used to represent the *TS* of single targets within the bin. The value of σbs_i used to estimate fish abundance in each proportion of school volume was assigned to every fish in that proportion of school volume such that every fish had a value of σbs that could later be converted to length.

In the next three scenarios, the same procedure was used to calculate the abundance of fish in schools. However, the *TS* values used to scale the *Sv* of the school differed. In these scenarios, a simulated value of *TS* was generated for each observed single target around a given school. In the first of these scenarios, *TS* values were simulated from a truncated normal distribution centered around the mean expected *TS* of all species observed on SRV cameras. Expected *TS* was estimated by converting lengths from the community census or FishBase using specific *TS*-length models, which are described in detail in the subsequent section and Table 1. The distribution was truncated by a lower value of either the smallest expected *TS* in the community census of a species that was observed on SRV cameras or the smallest expected *TS* converted from the length at maturity in FishBase of species observed on SRV cameras, and an upper value of the largest expected *TS* in the community census of a species that was observed on SRV cameras or largest *TS* converted from the maximum length in FishBase of species observed on SRV cameras. The standard deviation of the distribution was set to the standard deviation of expected *TS* among all species observed on the SRV cameras. The same procedure was followed to generate *TS* values for single targets around schools in the second and third of these scenarios, but using only expected *TS* values for small pelagic species (Atlantic Bumper *Chloroscombrus chrysurus*, Atlantic Spadefish *Chaetodipterus faber*, Bermuda Chub *Kyphosus sectatrix*, Blue Runner *Caranx crysos*, Gulf Menhaden *Brevoortia patronus*) in the second

scenario, and only expected *TS* values for large piscivorous species (Cobia *Rachycentron canadum*, Crevalle Jack *Caranx hippos*, Great Barracuda *Sphyraena barracuda*, Greater Amberjack *Seriola dumerili*, Horse-Eye Jack *Caranx latus*, King Mackerel *Scomberomorus cavalla*) in the third. Dense schools of fish at our study sites were typically composed of the species in scenario two (Bolser et al. 2020, 2021). However, we conducted scenarios one and three to evaluate the consequences of scaling school *Sv* with *TS* observations from species that may not have been represented within dense schools, yet were encountered in the surrounding area.

In all scenarios, the schools dataset was merged with the dataset of tracked fishes to represent the complete community of fishes sampled by the echosounder (i.e. water column fishes). Crypto-benthic fishes and fishes tightly-associated with the platform structure likely were not sampled by the echosounder due to our conservative treatment of the seafloor and platform structure, and inherent limitations of interpreting reverberation in rugose habitats.

Target Strength to Length Relationships

The *TS* of fish was converted to length in two ways to comprise two different datasets that we compared. For the first, the general *TS*-length model of Love (1971) was applied to all data to represent a situation in which no ground-truthing data were available and the species sampled were unknown. The *TS*-length model of Love (1971) for 120 kHz transducers is:

$$Length = 10^{TS+63.85/19.1}$$

For the second dataset, specific *TS*-length models were chosen based on the identity of the species recorded by SRV camera surveys (Table 1). A species-specific model was not available for each of the 29 observed species, so models for related species were used (same

species: 3 of 29; same genus: 5 of 29; same family: 21 of 29; same order: 29 of 29; Table 5.1). To apply these models, it was necessary to assign a species identity to each *TS* observation. We did this by (1) converting 'common length' from FishBase or mean length in the community census of each species to *TS* using the closest published *TS*-length formula for the observed species (Table 1); (2) ordering the species from smallest to largest predicted *TS* value, and similarly ordered the *TS* dataset from smallest to largest for each survey; (3) proportionally assigned *TS* observations a species identity in order based on the observed relative abundance of species; and (4) applying *TS*-length models to *TS* values by their assigned species to estimate lengths.

Table 5.1: Specific target strength (*TS*) to length models used for each species. Family and order names are included to show the relatedness of each species to the species on which the model was based.

Model (*reference*)	Species that the model is based on	Species that this model applied to
TS = 53.7*log(length) – 130.2 (*Foote 1980*)	*Scomber scombrus* (Scombridae, Scombriformes)	*Scomberomorus cavalla* (Scombridae*), Sphyraena barracuda* (Scombriformes), *Sphyraena guachancho* (Scombriformes)
TS = 20*log(length) – 80.4 (*Zhang et al. 2014 in: Rosenthal et al. 2014*)	*Epinephelus awoara* (Serranidae)	Serranidae spp. (Groupers were not consistently identified to genus or species)
TS = 20*log(length) – 65.4 (*Kang et al. 2004*)	*Acanthopagrus schlegeli* (Sparidae)	*Archosargus probatocephalus* (Sparidae)
TS = 19.9*log(length) – 66.7 (*Boswell et al. 2020*)	*Balistes capriscus* (Balistidae)	*Balistes capriscus, Canthidermis sufflamen* (Balistidae)
TS = 20*log(length) – 66.65 (*Hwang et al. 2015*)	*Trachurus japonicus* (Caragnidae,Caragniformes)	*Carangoides bartholomaei* (Caragnidae), *Carangoides ruber* (Caragnidae), *Caranx crysos*

		(Caragnidae), *Caranx hippos* (Caragnidae), *Caranx latus* (Caragnidae), *Chloroscombrus chrysurus* (Caragnidae), *Elagatis bipinnulata* (Caragniformes), *Oligoplites saurus* (Caragnidae), *Rachycentron canadum* (Caragniformes), *Selene setapinnis* (Caragnidae), *Selene vomer* (Caragnidae), *Seriola dumerili* (Caragnidae), *Seriola rivoliana* (Caragnidae)
TS = 17.1*log(length) – 60.3 (*Boswell et al. 2020*)	*Lutjanus campechanus*	*Lutjanus campechanus, Lutjanus grisus, Lutjanus jocu,*
TS = 18.2*log(length) – 65.8 (*Boswell et al. 2020*)	*Haemulon aurolineatum* (Haemulidae, Perciformes)	*Chaetodipterus faber* (Perciformes), *Kyphosus sectatrix* (Perciformes), *Pomatomus saltatrix* (Perciformes), *Scianops ocellatus* (Perciformes)
TS = 18.8 * log(length) – 62.4 (*Nakken and Olsen 1977*)	*Clupea harengus* (Clupeidae)	*Brevoortia patronus* (Clupeidae)
TS = 51.7*log(length) – 118.6 (*Boswell et al. 2020*)	*Rhomboplites aurorubens*	*Rhomboplites aurorubens*

Table 5.1 (continued)

Estimation of Size Spectra Slopes

Size spectra slopes for each dataset were calculated following the maximum likelihood estimation method of Edwards et al. (2017). Briefly, the slope of a bounded power law distribution fit to size distribution data is estimated, rather than binning data and estimating size spectrum slope with linear regression. In this method, the probability density function for the body size of an individual fish is:

$$f(x) = Cx^b, x_{min} \leq x \leq x_{max}$$

where,

$$C = \begin{cases} \dfrac{b+1}{{x_{max}}^{b+1} - {x_{max}}^{b+1}}, & b \neq -1 \\ \dfrac{1}{log x_{max} - log x_{min}}, & b = -1 \end{cases}$$

and *x* represents possible values of the body size of an individual fish, *log* is the natural logarithm, *b* is an exponent (the parameter that describes size spectrum slope), and x_{min} and x_{max} represent the minimum and maximum values of length or body mass (with $0 < x_{min} < x_{max}$) (Edwards et al. 2017). *C* is a normalization constant and is calculated by solving $\int_{x_{min}}^{x_{max}} f(x)dx = 1$ (Edwards et al. 2017).

Statistical Comparisons of Size Spectrum Slopes and Mean Lengths of Fishes Between Datasets

Non-parametric Kruskal-Wallis (KW) tests with Dunn's multiple comparison posthoc tests were used to determine significant differences between size spectrum slopes generated from each datase in R Studio (KW test: base 'stats' package, ver. 3.6.1; Dunn's posthoc test: 'FSA' package, ver. 0.8.31, Ogle et al. 2020). The same procedure was used to compare the mean length of fishes in each dataset.

Statistical comparisons were also conducted on all datasets except for the community census after they were filtered to include only surveys with good visibility for ground-truthing (SRV camera visibility score of > 2.0 out of 3.0; see Bolser et al. (2020) for scoring details) and a mean fish orientation angle (from tracked fishes, see below) within 2.0º of normal to the horizontal axis. The threshold for visual data was chosen based on the analyses of Bolser et al. (2021), who linked SRV camera and acoustic data and examined biases in a dataset containing the study platforms, and the threshold for orientation was chosen as a relatively conservative level that removed outlying slopes based on preliminary examination of the data. These analyses were also conducted for data thresholded bv visibility alone and orientation angle alone. Mann-Whitney-Wilcoxon rank sum tests were used to compare slopes and fish lengths between each type of full and reduced datasets in R Studio (base 'stats' R package, ver. 3.6.1). Results for these comparisons are presented in Appendix 4.

Examining the Influence of Fish Orientation on TS and Size Spectrum Slopes

We examined the impact of fish orientation relative to the acoustic transducer on our results using the orientation angle of tracked fishes ('Direction_vertical' in Echoview) in four ways. First, we calculated the mean and standard deviation of orientation angle and absolute angle of all tracked fish in a survey to determine if *TS* measurements were affected by orientation on average. Second, we used Gamma Generalized Linear Models (GLMs) with inverse link functions to examine the effect of orientation angle and absolute angle on *TS* (base 'stats' R package, ver. 3.6.1). Third, we investigated the effect of average orientation angle and absolute angle on size spectrum slopes using Gamma GLMs with log link functions (base 'stats' R package, ver. 3.6.1). These models were fitted to the absolute value of slope to facilitate the use of log link functions, which, after preliminary examination of data properties, were deemed to be

most appropriate for these datasets. Generalized additive models were also explored for the second and third analyses, but their fits were nearly identical to GLM fits, so GLMs were chosen for parsimony. Fourth, we employed the method of de Kerckhove et al. (2015) to quantify the coefficient of variation (CV) in size spectra estimates that was associated with variable estimates of *TS* due to variable fish orientation. This entailed randomly assigning each fish a new *TS* value by sampling from a truncated normal distribution (truncated to the *TS* thresholds; R package 'truncnorm', ver. 1.0-8) with a mean equal to its observed *TS* and a standard deviation equal to the standard deviation of *TS* of all fish tracks (de Kerckhove et al. 2015). This process was iterated 1000 times for each survey and the slope of the size spectrum for each of the 1000 datasets was estimated, followed by the calculation of the mean and standard deviation of slopes for each survey (de Kerckhove et al. 2015).

RESULTS

Comparison of Mean Fish Length in Each Dataset

Median fish lengths in all datasets were significantly different from one another (KW χ^2 = 7,107,693, $p < 0.0001$, df = 6; Fig. 5.1; Appendix 4). Median fish lengths from the community census and simulated communities were longer that lengths derived from acoustics, particularly those that were derived from scaling school *Sv* by *in situ TS* from single targets around schools, regardless of *TS*-length model type used (Fig. 5.1; Table 5.2; Appendix 4). Differences between median fish lengths in each simulated scenario for single targets around schools were small, though statistically significant (Fig. 5.1; Table 5.2; Appendix 4). Results for comparisons between median fish lengths in datasets that were filtered for water clarity and mean orientation are presented in Appendix 4, but briefly, excluding surveys with unsuitable water clarity for

ground-truthing or mean orientations of $> 2^{o}$ and $< -2^{o}$ did not result in conclusions that were different than those drawn from the full datasets.

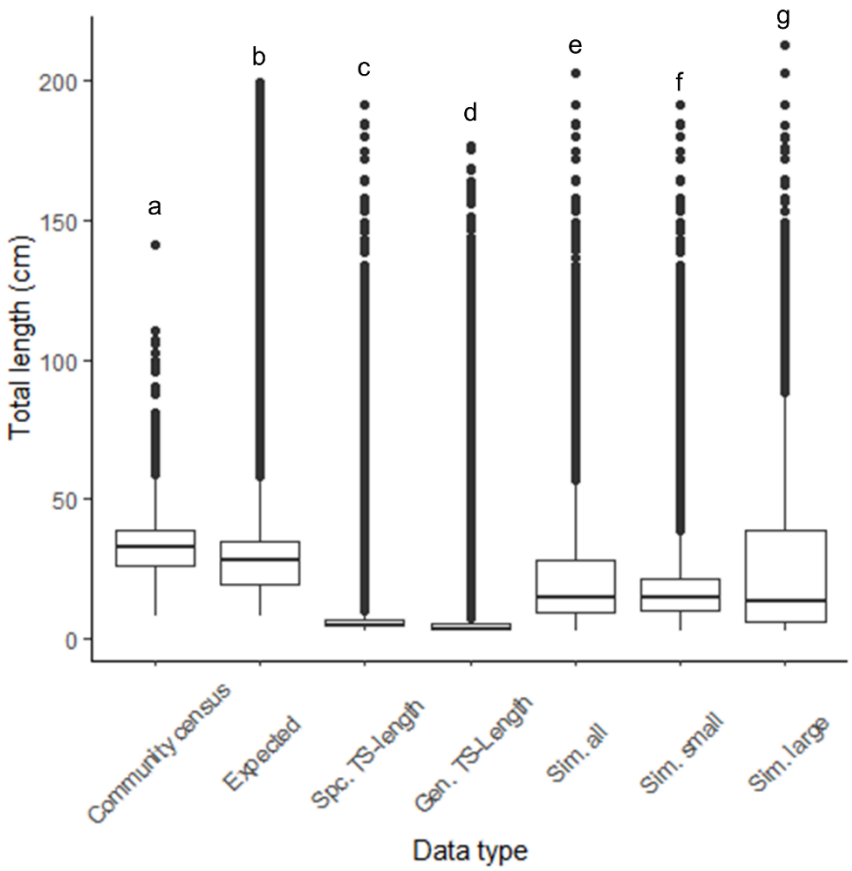

Figure 5.1: Boxplots of fish length. Letters indicate similar and different groups based on Dunn's Kruskal-Wallis multiple comparison posthoc test. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "Gen. TS-length" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Spc. TS-length" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Table 5.2: Median (standard deviation in parentheses) fish length (cm) in each dataset. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. full TS range" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small pelagic TS" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large piscivore TS" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Community census	Expected	Specific TS-length conversion	General TS-length conversion	Simulation: full TS range	Simulation: small pelagic TS	Simulation: large piscivore TS
32.50 (*10.83*)	27.87 (*15.71*)	4.74 (*6.03*)	3.48 (*4.67*)	14.80 (*16.59*)	14.80 (*9.79*)	13.30 (*33.02*)

Comparison of Size Spectra Slopes in Each Dataset

There were significant differences in size spectra slopes between datasets (KW χ^2 = 53.154, $p < 0.0001$, df = 3; Fig. 5.2; Appendix 4), with those derived from scaling school *Sv* by *in situ TS* from single targets around schools being significantly steeper than slopes derived from the other datasets (Fig. 5.2; Table 5.3; Appendix 4). Slopes from the community census, expected, and each simulated scenario for single targets around schools were not significantly different from one another (Fig. 5.2; Table 5.3; Appendix 4). Results for comparisons between median size spectrum slopes in datasets that were filtered for water clarity and mean orientation are presented in Appendix 4, but briefly, excluding surveys with unsuitable water clarity for ground-truthing or mean orientations of $> 2^{\circ}$ and $< -2^{\circ}$ did not result in conclusions that were different than those drawn from the full datasets.

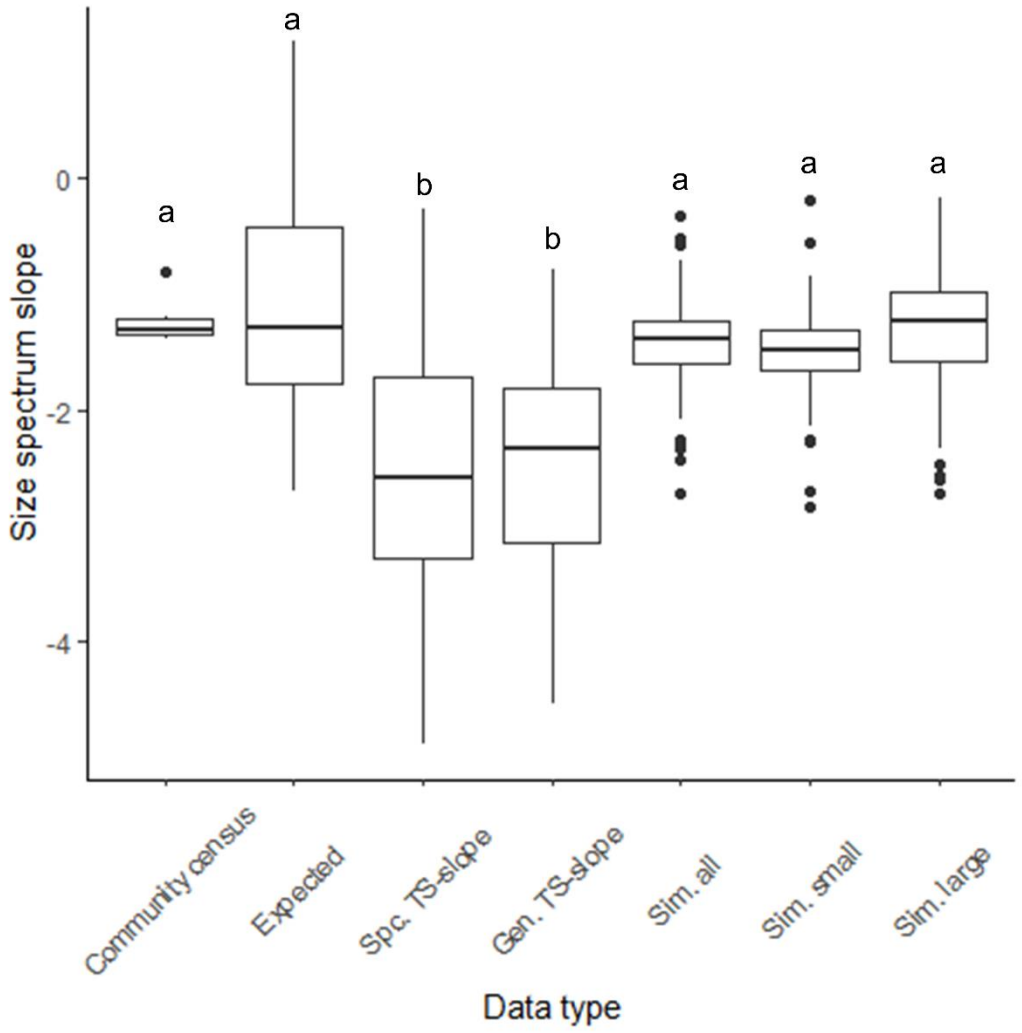

Figure 5.2: Boxplots of size spectrum slopes. Letters indicate similar and different groups based on Dunn's Kruskal-Wallis multiple comparison posthoc test. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "Gen. TS-length" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Spc. TS-length" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Table 5.3: Median (standard deviation in parentheses) size spectrum slope for each dataset. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. full TS range" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small pelagic TS" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large piscivore TS" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Community census	Expected	Specific TS-length conversion	General TS-length conversion	Simulation: full TS range	Simulation: small pelagic TS	Simulation: large piscivore TS
-1.31 (*0.21*)	-1.29 (0.90)	-2.59 (*1.12*)	-2.33 (*0.88*)	-1.38 (*0.48*)	-1.48 (*0.45*)	-1.24 (*0.57*)

Influence of Fish Orientation on Hydroacoustic Size Spectra

While fishes generally were oriented horizontally (mean = 0.3º), there was considerable variation (SD = 15.6º). The mean absolute value of orientation angle for all tracked fishes was 10.4º (± 11.6º). Despite significant *p*-values, the low adjusted-R^2 values of Gamma GLMs indicated that orientation angle (adj. $R^2 = 3.47e^{-5}$, $p < 0.01$) and the absolute value of orientation angle (Adj. $R^2 = 2.87e^{-3}$, $p < 0.001$) did not have a meaningful effect on *TS* in our dataset. Mean orientation angle did not have a significant effect on size spectrum slope in the Gamma GLM fit to the specific *TS*-length model dataset (adj. $R^2 = 0.01$, $p = 0.20$) or in the Gamma GLM fit to the general *TS*-length model dataset (adj. $R^2 = 0.03$, $p = 0.09$). Similarly, mean absolute orientation angle did not have a significant effect on size spectrum slope in the Gamma GLM fit to the specific *TS*-length model dataset (adj. $R^2 = 0.01$, $p = 0.06$) or in the Gamma GLM fit to the general *TS*-length model dataset (adj. $R^2 = 0.01$, $p = 0.10$). In our simulations designed to assess

the influence of *TS* variation due to variable fish orientation on size spectra slopes, the average CV of *TS* variation on size spectrum slope was 0.6% in the General *TS*-length dataset and 0.8% in the specific *TS*-length dataset.

DISCUSSION

Assessing fish community size spectra in rugose marine habitats such as the petroleum platforms we sampled involves numerous challenges related to the conversion of *TS* to length, assigning a species identity to *TS* observations, and scaling the *Sv* of schools to fish density and abundance. We found that fish lengths and size spectra slopes were underestimated by acoustics compared to censused communities and the expected values of these metrics based on species composition when *in situ TS* was used to scale the *Sv* of schools (Figs. 5.1 & 5.2). However, acoustic size spectra slopes were comparable to non-acoustic slopes when simulated values representing different assumptions about the species composition of single targets around schools were used for scaling school *Sv*. While we did not find that fish orientation affected *TS* or size spectra slopes in the datasets as a whole, orientation likely had a role in explaining the differences between the datasets that employed *in situ TS* measurements for school *Sv* scaling and those that employed simulated data.

There is a large body of literature documenting the influence of orientation angle on *TS*, and thus estimated fish size, for individuals of a single species (e.g. Nakken and Olsen 1977; McClatchie et al. 1996b; Simmonds and MacLennan 2008). The effect of orientation on *in situ TS* in mixed species assemblages has received less attention but could be an important source of uncertainty in acoustic size spectra studies. We did not find that orientation or absolute orientation had effects on size spectra slopes or *TS* in GLMs fit to our data or simulations designed to assess the effects of orientation. Accordingly, the effect of variation in fish length on

TS was likely larger than the effect of variation in orientation on *TS* in the diverse communities we sampled. However, many *in situ TS* observations of single targets around schools were smaller than predicted based on the expected TS of the species observed – even in the scenario in which single targets around schools comprised only small pelagic fishes – resulting in measures of center for *in situ TS* distributions around schools that were also smaller than in any simulated scenario. It is likely that these discrepancies are due to fishes around schools having orientations that were not normal to the horizontal axis, or the presence of non-fish scattering sources.

Discrepancies in the *TS* distributions of single targets around schools are exacerbated when they are used to scale the *Sv* of schools to fish abundance. When *TS* is underestimated (e.g. when fish orientation is far from normal to the horizontal axis) and used for school *Sv* scaling, fish density and abundance values greatly increase. Further, in our procedure, these numerous schooling fishes would have also been assigned the small *TS* of the single targets around schools. Comparatively larger numbers of small fish in a community results in steeper size spectra slopes, as was observed when datasets that employed *in situ TS* measurements to scale school *Sv* were compared with other datasets (Fig. 5.2, Table 5.3).

Scaling school *Sv* with *in situ* or simulated *TS* data involves making significant assumptions about the degree to which those data represent the *TS* of fishes within schools. It was not possible to directly test the validity of those assumptions by measuring the lengths of fishes in the present study, but our three simulations for the *TS* distribution of single targets around schools was designed to represent three scenarios based on our species compositions: (1) that single targets around schools were composed of all species observed on SRV cameras, (2) that single targets around schools were composed of the small pelagic species that typically formed dense fish schools, and (3) that single targets around schools were composed of large

piscivorous species that may prey upon the small pelagic schooling species. Size spectra slopes and fish lengths estimated each of in the scenarios were similar to one another (though fish lengths were statistically different, likely due to large sample sizes; Fig. 5.1, Table 5.1, Appendix 4), and each scenario produced size spectra slopes that were comparable to those derived from non-acoustic data. This contrasts with the results for the datasets that employed *in situ TS* distributions to scale the *Sv* schools, which exhibited size spectra slopes that were significantly steeper than all other datasets – possibly due to the effect of fishes around schools not being normally oriented to the horizontal axis, as discussed above. Accordingly, we propose that the orientation of fishes around schools may be more impactful than their species identity when using their *TS* to scale school *Sv* and estimate acoustic size spectra.

Fish lengths were shorter in acoustic datasets than in non-acoustic datasets, even when simulated values were used to scale school *Sv*. A possible explanation for this is the presence of large numbers of bladder-less fishes in the communities we sampled (Bolser et al. 2020, 2021). Bladder-less fishes (e.g. caragnids) have significantly weaker *TS* than fishes of a similar size with a swim bladder (Foote 1980; McClatchie et al. 1996a; Simmonds and MacLennan 2008), and although the general *TS*-length model of Love (1971) was based on empirical data from different species of fishes with and without swim bladders, the proportion of bladder-less species was likely larger at our study sites than in the samples of Love (1971). Even if the proportion of bladder-less fishes in our dataset is not considered, the comparability of the general *TS*-length model of Love (1971) and other *TS*-length models or measured lengths for fishes with bladders varies depending on size class and species (e.g. Fleischer et al. 1997; Mehner 2006; Wanzenböck et al. 2020). While we did not estimate the length of a bladder-less fish with a model based on a fish with a swim bladder and vice-versa in the specific model dataset, the size range of the

species a model was applied to often exceeded the size range of the species that the model was developed for. Results derived from the general *TS*-length model of Love (1971) and the specific *TS*-length models we employed were similar, but clearly, more work must be done to develop specific *TS*-length models for more species in our study area (e.g. Boswell et al. 2020), as each species did not have its own specific model. Species-specific models that are designed to incorporate the effect of orientation angle on *TS* would be particularly desirable and would help definitively identify the source of discrepancies in fish length between acoustic and other methods in size spectra studies.

Our procedure for applying specific *TS*-length models involved some non-trivial assumptions. We sorted *TS* from smallest to largest, ranked species from smallest to largest based on their expected *TS*, and used those orders to assign each *TS* observation a species identity. As identified above, the *TS* of a small bladdered fish could overlap with the *TS* of a larger bladder-less fish. If this occurred, an incorrect *TS*-length model could have been applied, which could substantially affect length estimates. Possible examples of this occurring may be found in the outlying points in Fig. 5.1. Considering that the size spectrum slopes were comparable between the datasets that employed simulated *TS* for scaling school *Sv*, we propose that discrepancies in fish length between acoustic and non-acoustic datasets are most likely due to the *TS*-length models systematically underestimating the length of individuals in all size classes (in addition to the substantially higher numbers of small fishes in the dataset employing *in situ TS* measurements to scale school *Sv*). Bladder-less fishes were found in nearly all size classes at our study sites, and if their lengths were consistently underestimated, it is possible that median length could be significantly shorter in acoustic datasets while size spectra slopes were comparable.

To fully validate acoustic size spectra, they must be directly compared with data derived from other methods applied at the same time and place. This was not possible in our study given the numerous logistical constraints associated with surveying fish communities at marine petroleum platforms. However, the platform community census data (Gitschlag et al. 2001) provided a useful reference that was likely free of significant gear bias. Given the lack of significant differences in size spectra slopes between the community census data and our expected size distributions, our method of generating simulated communities based on relative abundance data from our SRV camera, the community census, and FishBase data provided a reasonable representation of platform fish communities. However, it is possible that fish communities at platforms have changed in the last ~ 20 years, particularly given the high fishing pressure petroleum platforms experience (Schuett et al. 2016; Cowan and Rose 2016; Stunz and Coffey 2020), which alters size structure of fish communities by making larger fishes less represented (Mason 1998; Jennings and Kaiser 1998; Berkeley et al. 2004). This would result in steeper size spectrum slopes (Pope and Knights 1982; Blanchard et al. 2009; Robinson et al. 2017), as we observed in the acoustic datasets that employed *in situ TS* to scale school *Sv*. It is also possible that size distributions among platforms varied throughout our study area, confounding the comparison of our data with the community census data, which were collected over a relatively narrow spatial range. Indeed, Egerton et al. (2021) reported spatial differences in the mean *TS* of fishes surrounding GOM petroleum platforms, which were associated with variation in salinity and temperature between study sites. Future work should extend validation efforts to direct comparisons between different gear types in marine environments, as has been done in freshwater systems (Coll et al. 2007; de Kerckhove et al. 2015; Daigle 2017), to determine the degree to which the discrepancies we observed were due to assumptions and

uncertainty associated with using acoustic data to assess fish community size spectra, or actual differences in communities over time and space.

The results of prior studies validating the measurement of size spectra with acoustics in freshwater environments through comparisons with other gears have been inconclusive when considered as a whole (Coll et al. 2007; de Kerckhove et al. 2015; Daigle 2017). We were unable to find direct comparisons of size spectra slopes between acoustics and other gears in the literature, although size distributions may be reasonably comparable between acoustics and netting approaches in some cases, depending on selectivity, sampling locations, and treatment of tracked fish *TS* (Coll et al. 2007; de Kerckhove et al. 2015; Daigle 2017). Acoustically-derived lengths have been shown to be shorter than those estimated by netting (Coll et al. 2007; Daigle 2017) and fishery data (Coll et al. 2007), although it is difficult to identify actual discrepancies from the effects of selectivity in these studies. Our finding that acoustics underestimates length agrees with prior findings (Coll et al. 2007; Daigle 2017), suggesting that selectivity may not have been a major determinant of their results. However, those studies employed the general *TS*-length model of Love (1971). Thus, it is possible that the acoustic results could have changed if specific *TS*-length models were applied.

The size spectra slopes we estimated with acoustics around marine petroleum platforms were generally less steep than size spectrum slopes estimated with acoustics in lakes (Wheeland and Rose 2015; de Kerckhove et al. 2015; Daigle 2017; range of cited studies: 9.22 to -0.4), and steeper than slopes estimated with acoustics in rugose marine habitats (Egerton 2017; -0.38 to -0.03). It should be noted, however, that the size spectra reported by Egerton (2017) exhibited domes, which complicates interpretation of slopes. Studies that assessed marine fish size spectra in rugose marine habitats employing non-acoustic methods generally showed slopes that were

less steep or similar to those derived from acoustic data in the present study (e.g. Graham et al. 2005, 2007; McClanahan and Graham 2005; Wilson et al. 2010; Robinson et al. 2017; range of cited studies: -1.95 to -0.03). While it is difficult to make quantitative comparisons between our results and other studies because of methodological differences (e.g. method of calculating slope; Robinson and Baum 2015; Edwards et al. 2017), our results were more similar to studies in rugose habitats using other gears than they were to studies in different habitats using hydroacoustics. This qualitative comparison, along with our quantitative comparisons of acoustic size spectra slopes with slopes derived from the community census and simulated communities at petroleum platforms, suggest that differences between our findings and published size spectra slopes in rugose habitats may be better explained by actual differences in community structure than differences in methodology (when simulated values were used to scale school *Sv*).

Despite reasonably favorable comparisons with non-acoustic data when simulated values were used to scale school *Sv*, it is clear that more research is needed before acoustic data are used to make scientific inferences or management decisions for fish communities in rugose marine habitats such as those we sampled at petroleum platforms. Along with the development of *TS*-length models for additional species that incorporate orientation and further comparisons with non-acoustic data, future work should investigate the potential for assigning a species identity to fish within schools based on school characteristics (e.g. Horne 2000; Simonsen 2013; Campanella and Taylor 2016) and otherwise determine the optimal source of *TS* data for scaling school *Sv*. We view further research effort in these areas as worthwhile considering how rapidly acoustic data can be collected, which would make acoustic size spectra slopes efficient indicators that could be assessed frequently over large spatial and temporal scales. Although assessing size spectra with acoustics at petroleum platforms and other rugose marine habitats with large

numbers of bladder-less and schooling fishes presents numerous challenges relative to other situations, fish communities in these areas can be highly dynamic, are affected by a variety of natural and anthropogenic stressors, and can support economically-important fisheries, thus making the monitoring fish community dynamics in these areas is important. For example, fish communities at petroleum platforms in the Gulf of Mexico vary seasonally (Stanley and Wilson 1997; Barker and Cowan 2018; Reynolds et al. 2018), are affected by numerous environmental variables, particularly those related to freshwater inflow and circulation patterns (Gallaway and Lewbel 1982; Munnelly et al. 2020; Bolser et al. 2021), are subject to high levels of fishing pressure (Schuett et al. 2016; Cowan and Rose 2016; Stunz and Coffey 2020), and have been increasingly affected by decommissioning procedures, resulting in a net decrease in standing platforms over the last decade (Gitschlag et al. 2001; LGL 2019; Munnelly et al. 2020). Assessing fish community size spectra with acoustics at platforms and similar habitats would allow the effects of these influences on fish community structure to be efficiently summarized in a standardized manner, allowing for powerful spatio-temporal comparisons.

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Chapter 6: Conclusions and Applications

Fisheries assessments rely on accurate estimates of life history parameters and a combination of fishery-dependent and fishery-independent data to estimate stock abundance and productivity. Fish life history traits, population processes, and community dynamics are affected by physical conditions (Conover and Present 1990; Jennings et al. 2009; Dickey-Collas et al. 2010; Zwolinski and Demer 2012; Secor 2015). Thus, physical drivers affect the data that inform fisheries assessments, even if they are not explicitly incorporated into the assessment process. Unless a concerted effort is made to do so, it may be difficult to separate the influence of methodological biases from physical conditions. This affects quantification of uncertainty in assessments and collective inferences about biological or ecological processes. If data that inform assessments are compromised by unaccounted variation, the consequences can cascade through assessments and adversely influence predictions. In this dissertation, I illustrated the effects of physical drivers and methodological biases at multiple levels of biotic organization that inform fisheries and ecosystem assessments. Biases that occur at the individual level may have the most severe consequences for assessment and management, yet unaccounted effects and biases in population and community data may also have consequences. Here, I explain those consequences, provide recommendations, and describe applications for the methodology and findings described in this dissertation.

In Chapter 2, I demonstrated how sampling bias can lead to incorrectly specifying growth parameters and showed how this affects per-recruit assessments. These findings are likely to be relevant for all exploited fish stocks; large and old individuals become increasingly scarce under heavy fishing pressure (Mason 1998; Jennings and Kaiser 1998; Berkeley et al. 2004), and are thus increasingly difficult to sample for age and growth studies. When these individuals are not present in samples, the maximum length term present in most growth models is underestimated. Since growth rate is inversely related to maximum length, individuals are estimated to grow faster in these fished populations. This creates a positive feedback loop: fish stocks may be estimated to be more productive than they actually are, leading to increases in allowable catch, which further

truncates age and length, resulting in further increases in estimated growth rate and productivity, continuing the cycle towards fishery collapse.

Our simple diagnostic of simulating observations to make sample size equal at age is useful for detecting and accounting for sampling biases. To reduce biases in future studies, sampling should be conducted such that a representative distribution of lengths at each age is generated, and simulations should be used to balance the distribution of samples at age. These simulations should result in a uniform distribution – as demonstrated in Chapter 2 – rather than a distribution that mimics a more complete sampling scenario using traditional gears, or even the true population structure. For example, Gwinn et al. (2010) recognized the problems associated with a lack of representation of large and old individuals and examined different sampling and bias-reduction strategies for their effects on growth parameter estimates through simulations. The study found that biases in growth parameter estimates pervaded all scenarios tested, including a scenario without size-selective sampling (i.e., the gear sampled the population structure without bias). Additionally, a subsequent study on Hawaiian snapper growth that employed our approach reinforced our conclusions (Scherrer et al. 2021). Scherrer et al. (2021) employed several growth modelling approaches to multiple datasets, including Bayesian methods, which are often employed to overcome deficiencies in sampling. However, when Scherrer et al. (2021) made sample size equal at age and fitted growth models, only 2 of 11 growth models produced parameter estimates that were within the 95% confidence intervals of growth parameter estimates generated from the raw data. Thus, employing our diagnostic method revealed that sample distribution had a quantifiable impact on their results.

The approach described in Chapter 2 is particularly applicable for studies attempting to describe spatio-temporal variation in growth, including documentation of the effects of physical conditions on growth, and fisheries-induced evolution. On the surface, the effects that we documented – namely faster growth rates and smaller sizes in a highly-exploited population – may be interpreted as an example of fisheries-induced evolution. However, at least in the case of the Gulf Corvina, it is not likely that fish became incapable of growing to their historic lengths over

their timeline of heavy exploitation; it is more likely that they are simply harvested before attaining those lengths. Indeed, the more parsimonious explanation in this, and potentially many other situations, is that sampling is being affected rather than the biology of a species. There are certainly excellent studies documenting fisheries-induced evolution on life history parameters (e.g. Kuparinen and Merilä 2007; Kuparinen and Hutchings 2012; Heino et al. 2015), yet caution should be taken when attempting to describe fisheries-induced evolution or spatio-temporal variation in growth using growth modelling approaches alone – particularly when sample distributions are different over time and space, which is often the case. Our quantification of sampling bias facilitates future descriptions of spatio-temporal variation in fish growth, which is inherently driven by physical conditions and may be influenced by selective fishing.

Physical conditions can drive some species to shift their geographic distributions, yet others may use physiological or behavioral mechanisms to cope with changes to their environment (Rijnsdorp et al. 2009; Secor 2015; Habary et al. 2017). My work in Chapter 3 provides the basis for predicting distribution shifts of important fishery species (e.g., Red Snapper, Greater Amberjack, Vermilion Snapper) in response to changes in physical conditions. However, the majority of the species examined were present at platforms across a wide range of platform characteristics and environmental conditions. This follows logically as the GOM is a dynamic ecosystem that experiences seasonal fluctuations in physical conditions and relatively frequent extreme weather events. Natural reef habitat is scarce (Parker et al. 1983), and accordingly, it is possible that some GOM reef-associated fishes have evolved physiological mechanisms to tolerate a wide range of physical conditions in order to take advantage of reef habitat. Alternatively, fishes may remain at the edges of their physiological tolerance to remain structure-associated, which may have consequences for individual fitness (Schulte 2014; Holt and Jørgensen 2015; Brownscombe et al. 2017). The range of many variables measured in Chapter 3 are unlikely to cause physiological stress to most fishes, but stressful effects could manifest from the levels of dissolved oxygen measured, for example. Growth and reproductive parameters (e.g., growth rate, fecundity), which are directly incorporated into fisheries assessments, are deleteriously affected if fishes are exposed

to stressful conditions (Thomas et al. 2007; Schreck and Tort 2016; Bolser et al. 2018). Accordingly, the findings described in Chapter 3 are useful for identifying species whose life history parameters and population dynamics may be most affected by changes to climate and habitat, thus also identifying the assessments that are most at risk of being compromised by unaccounted effects of physical conditions. However, laboratory experiements are needed to confirm physiological effects (e.g., blood oxygen binding assays for determining tolerance to hypoxia).

While life history parameters and distributions provide a foundation for fisheries assessments, the primary goal of most assessments is to estimate fish abundance and biomass. Chapter 4 provides data on the abundance – and variation in abundance – of important fishery species around platforms at a time when the abundance of some species throughout the GOM is under debate (e.g., Red Snapper *Lutjanus campechanus*: 'The Great Red Snapper Count' vs. recent stock assessments; NOAA Fisheries 2020). While the results of 'The Great Red Snapper Count' have not been made public yet, preliminary statements from the U.S. Congress indicate that Red Snapper abundance is 2 to 3 times greater than estimated by SEDAR (2018). In such large-scale sampling efforts, the sampling area is often stratified and a limited number of sites are used to characterize larger areas or habitat types. I found that the abundance of common platform-associated species, including Red Snapper, is highly variable from platform-to-platform. If this is also the case for the low-relief habitats at which Red Snapper are commonly encountered, the effect of methodological biases and differences in sampling strategy between the two groups that enumerated Red Snapper in the GOM could have been magnified, helping to explain their vastly different conclusions. It is likely that a similar independent effort will be undertaken to enumerate Greater Amberjack in the GOM and U.S. South Atlantic (Florida Seagrant 2020), and my findings in Chapter 4 suggest that the high degree of variability in Greater Amberjack abundance at platforms should be considered in the sampling strategy.

Along the continuum from single-species to ecosystem-based fisheries assessments, it becomes increasingly important to collect data on other metrics (e.g. diversity, size structure) of

fish communities in conjunction with abundance and biomass data. In Chapter 4, I demonstrated the application of combined optic-acoustic surveys to describe multiple fish community metrics at petroleum platforms and examined how physical conditions affected them. As discussed in relation to Chapter 3, association with habitat may be more important than optimal abiotic environmental conditions for explaining the distributions of many GOM platform-associated fishes. However, petroleum platforms have been removed at a rate greater than they have been installed over the last decade (BOEM 2019; Munnelly et al. 2020). Reduced habitat availability may make shifting distributions more challenging and may intensify the consequences of fitness reductions in species that are less likely to shift their distributions through increases in competitive interactions. Where platform-associated fish stocks as a whole are concerned, my findings in Chapter 4 suggest that these effects will disproportionately impact areas offshore of the Atachafalaya River. Platforms in this area have relatively higher fish biomass, density, diversity, and richness than platforms in nearshore areas and east of the Mississippi River, so reducing the number of platforms in this area would have an impact on a greater number of platform-associated species and individuals. Thus, it would be beneficial to prioritize efforts to preserve platform habitat, such as the Rigs to Reefs Program, in areas offshore of the Atachafalaya River.

Often, conclusions of studies conducted at small scales (e.g., less than 10 platforms within tens of kilometers) are extended to describe platform-associated fish communities and the factors that affect them throughout the GOM. This may be problematic, as different conclusions can be drawn regarding the influence of a particular physical condition due to differences in scale between studies, even if methodology is similar (e.g., the effect of salinity on Red Snapper distribution described by Munnelly et al. 2019 vs. Chapter 3). I illustrated this phenomenon by subsetting my own dataset and re-examining fish distributions in Chapter 4. The influence of scale in ecology is well-known (Levin 1992), and scale-dependence of the effects of physical conditions is particularly important to keep in mind in studies that take place in the dynamic GOM.

My conclusions would not have been possible without the examination of multiple metrics with complementary technologies at a large scale. One notable example of this is the effect of

salinity on platform-associated fish communities in the GOM, which was examined in Chapters 3 and 4. Waters of low salinity in the GOM commonly have poor water clarity, and while steps can be taken to reduce the influence of water clarity (e.g., examining encounter/non-encounter instead of abundance, including visibility score as a random effect term), it may still confound estimates of the effects of salinity when using camera-based studies. Accordingly, we also examined the influence of salinity on acoustically-derived metrics (e.g. acoustic measures of fish biomass, density, and size), and because it had a significant influence on multiple acoustics-based and camera-based metrics, we were able to confirm that salinity is an important driver of variation in platform-associated fish communities.

Gaining a detailed understanding of life history parameters and the effects of physical conditions on fishes through large-scale studies is important for conducting accurate fisheries assessments, yet employing efficient indicators of change can also be useful. Indeed, in both systems described in this dissertation – the Gulf Corvina stock threatened by increasing size truncation and the platform-associated fish communities affected by declining habitat and other changes in physical conditions – regular monitoring is required to detect changes in population and community structure, and to test inferences regarding the influence of physical conditions on those changes. Since funds may be limited for extensive data collection programs, it can be beneficial to develop sensitive indicators that may be assessed rapidly in order to prioritize more intensive research effort. I suggest that assessing the size spectra of fish populations and communities with hydroacoustics is an efficient way to meet this need. In Chapter 5, I found that hydroacoustic size spectra may be compared with size spectra derived through other means when simulated values are used to scale school *Sv* to fish density. While there are additional studies and direct comparisons to be made before hydroacoustic size spectra can be applied for scientific inferences of management decisions, my work quantifies the effects of various aspects of assessing size spectra with hydroacoustics that have inhibited the application of the technology to describe size spectra in rugose marine habitats in the past. Thus, my work in Chapter 5 advances the

application of size spectrum slope as an efficient indicator of the effects of fishing and physical conditions on marine fish populations and communities.

Unaccounted or incorrectly specified variability in data that feed fisheries assessments can propagate through assessments and compromise predictions. However, when these sources of variation are accounted for and quantified, the predictive power of assessments is improved, and it becomes more feasible to incorporate spatial and ecosystem considerations. By providing examples of limiting and quantifying methodological biases and challenges, and conducting large-scale studies of the effects of physical conditions on fishes, this dissertation provides information that may be applied in future spatial or ecosystem-based assessments in the GOM, GOC, and elsewhere.

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Appendicies

APPENDIX 1: SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Appendix 1.1. Details of the per-recruit model developed for Gulf Corvina (*Cynoscion othonopterus*)

We developed a parsimonious, non-spatial, per-recruit model for Gulf Corvina (*Cynoscion othonopterus*), which estimates the female spawning-stock-biomass-per-recruit (SSBR) and yield-per-recruit (YPR) of the species in relation to the annual exploitation rates of its old adults (≥ 5 year-old individuals; E_{OA}). Our model assumes that Gulf Corvina is harvested only during the spawning season (based on the results of Erisman et al. (2012b)), and that all the juveniles and young adults of Gulf Corvina (i.e., 0-4 years old individuals) escape fishing and the annual fishing mortality rate of these life stages due to bycatch is negligible (based on Walsh et al. (2004), Erisman et al. (2012a) and Pérez-Valencia (2012)). Our model also makes the assumption that the "encierre" technique used by the Gulf Corvina fishery means that there is no upper size limit to the fishery (i.e., large individuals do not escape capture); this assumption is supported by several lines of evidence, as described in detail in Erisman et al. (2014).

In the following, we first present the alternative assumptions we made regarding the growth in length and weight of Gulf Corvina in the per-recruit model. Then, we detail the calculation of SSBR, YPR and the current value of E_{OA} for Gulf Corvina. Finally, we describe the estimation of reference points for the species.

Growth in length and weight

In the per-recruit model, Gulf Corvina is assumed to grow according to one of five alternative growth models (Figure S1): (1) the von Bertalanffy model developed in Gherard et al. (2013), referred to as the "Gherard model"; (2) the von Bertalanffy model fit to raw data in the

present study; (3) the von Bertalanffy model fit to raw data bolstered by simulation values in this study; (4) the Schnute-Richards model fit to raw data in the present study; and (5) the Schnute-Richards model fit to raw data bolstered by simulation values in this study. The Gherard model assumes the following relationship between length L (in mm TL) and age a (in years):

Eq. S1.1: $$L(a) = 1006 * [1 - e^{-0.225(a-0.616)}]$$

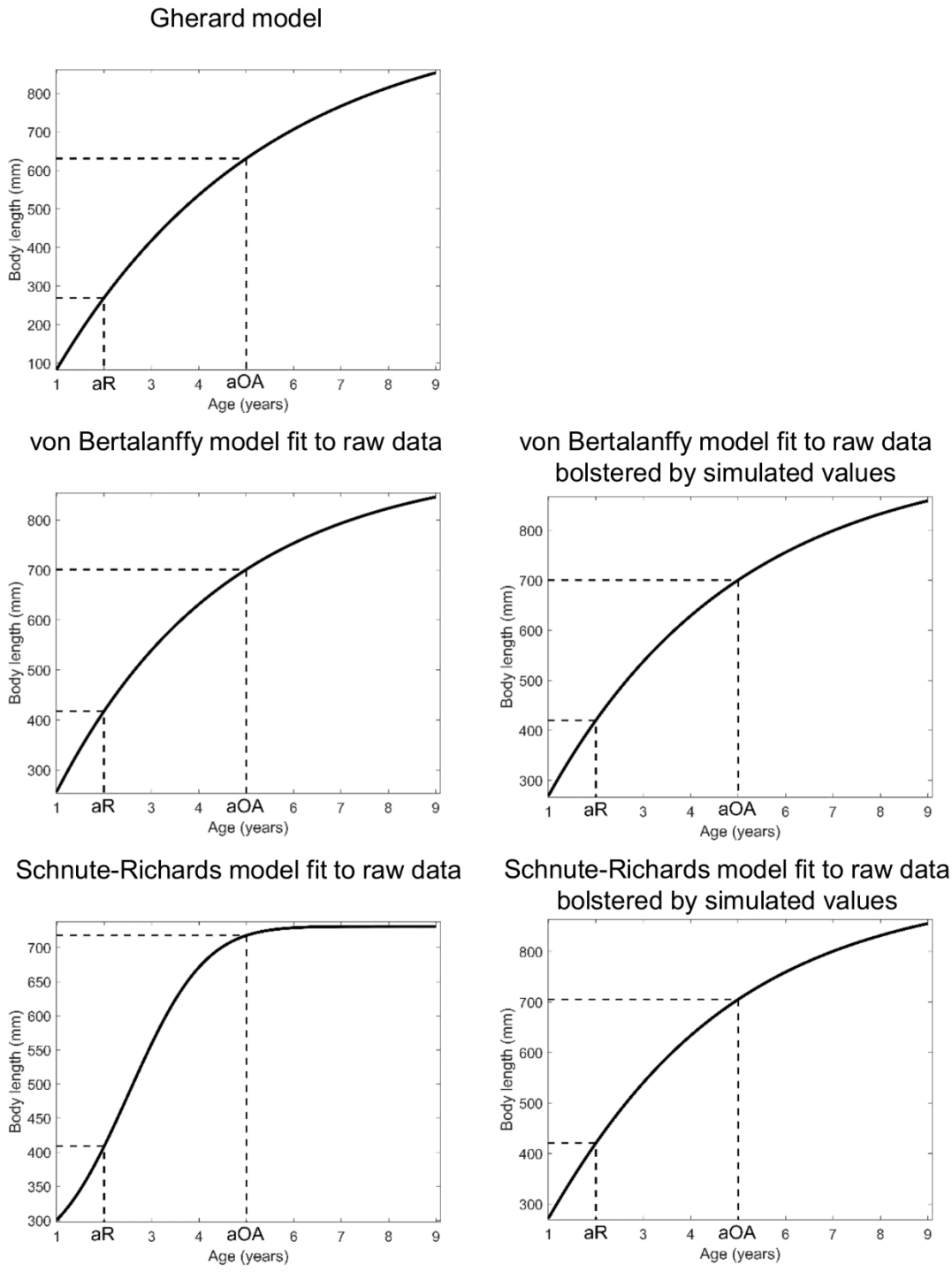

Figure S1. Alternative length-at-age models for Gulf Corvina

The body weight of Gulf Corvina at age a, $w(a)$, is calculated from the length-at-age predicted by one of the five growth models as follows (Figure S2; Gherard et al., 2013):

Eq. S1.2: $$w(a) = 2 * 10^{-5} * L(a)^{2.8834}$$

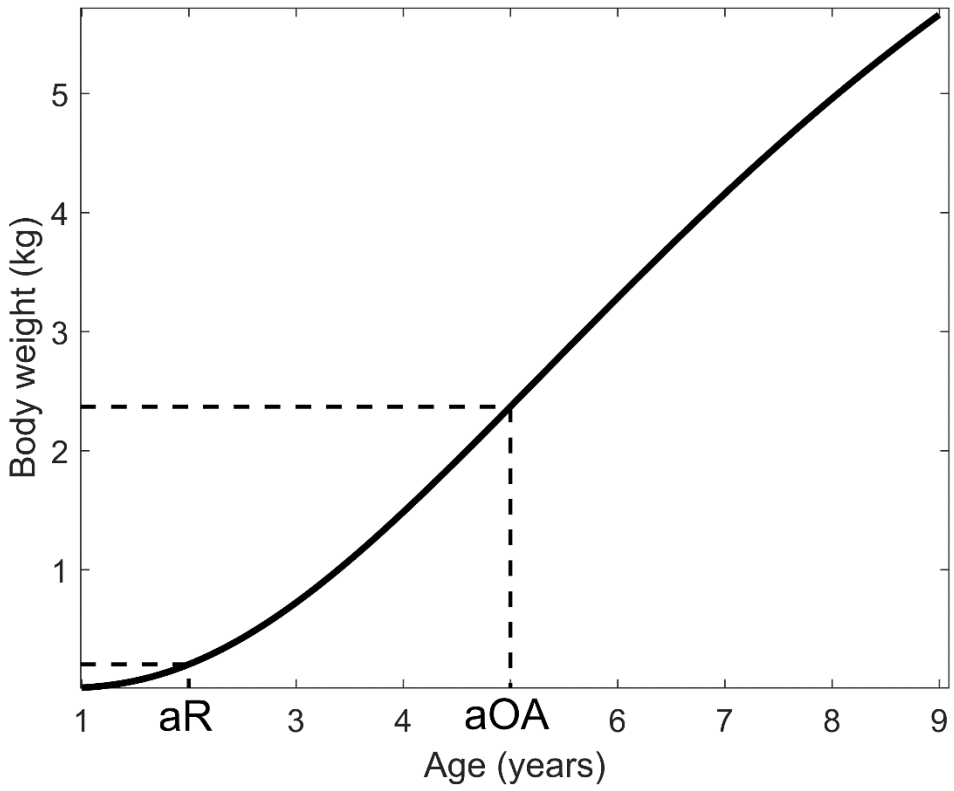

Figure S2. Weight-at-age model for Gulf Corvina

Estimation of SSBR, YPR and the current value of E_{OA}

Our per-recruit model estimates SSBR as follows:

Eq. S1.3: $$SSBR = \frac{SR}{1+SR}\int_{a_R}^{a_{OA}} e^{-M(a_R-0)}e^{-M(a-a_R)}w(a)da + \frac{SR}{1+SR}\int_{a_{OA}}^{a_{MAX}} e^{-M(a_R-0)}e^{-M(a_{OA}-a_R)}\left[e^{-M(a-a_{OA})}(1-E_{OA})^{(a-a_{OA})}\right]w(a)da$$

where SR is the female:male sex ratio of Gulf Corvina (which is assumed to be 1:1 for the sake of simplicity); M is the natural mortality rate (0.28 year^{-1}; estimated in Erisman et al. (2014) using Pauly (1980)'s relationship); E_{OA} is the exploitation rate of old adults (in year^{-1}) (and, therefore, $(1-E_{OA})$ is the escapement rate of old adults (in year^{-1})); a_R is the age of sexual maturity (2 years; Gherard et al., 2013); a_{OA} is the age of transition from the young adult stage to

the old adult stage (i.e., 5 years); and a_{MAX} is the maximum age (9 years; Gherard et al., 2013). It is reasonable to use exploitation rates rather than the more conventional fishing mortality rates for young and old adults of corvina, because the Gulf Corvina fishing season is very short (Erisman et al., 2014).

YPR is estimated by our pre-recruit model as follows:

Eq. S1.4:
$$YPR = E_{OA}\int_{a_{OA}}^{a_{MAX}} e^{-M(a_R-0)}e^{-M(a_{OA}-a_R)}\left[e^{-M(a-a_{OA})}(1-E_{OA})^{(a-a_{OA})}\right]w(a)da$$

To determine the current value of E_{OA} for Gulf Corvina, we compiled length data from 2013-2015 to create a length frequency distribution. Then, we determined that E_{OA} is equal to 0.825 year^{-1}, based on combinations of M (Pauly, Hoenig) and three methods to calculate the total mortality rate of Gulf Corvina (Seine, LDFA, catch curves). Calculation of this rate is explained in greater detail in Erisman et al. (2014).

Estimation of reference points

So as to facilitate the discussions of our results, we estimated two reference points for Gulf Corvina with our per-recruit model: the maximum value of the YPR of Gulf Corvina, YPR_{max}; and the natural SSBR of Gulf Corvina (NSSBR), i.e., its SSBR in the absence of fishing (Figures S3 and S4).

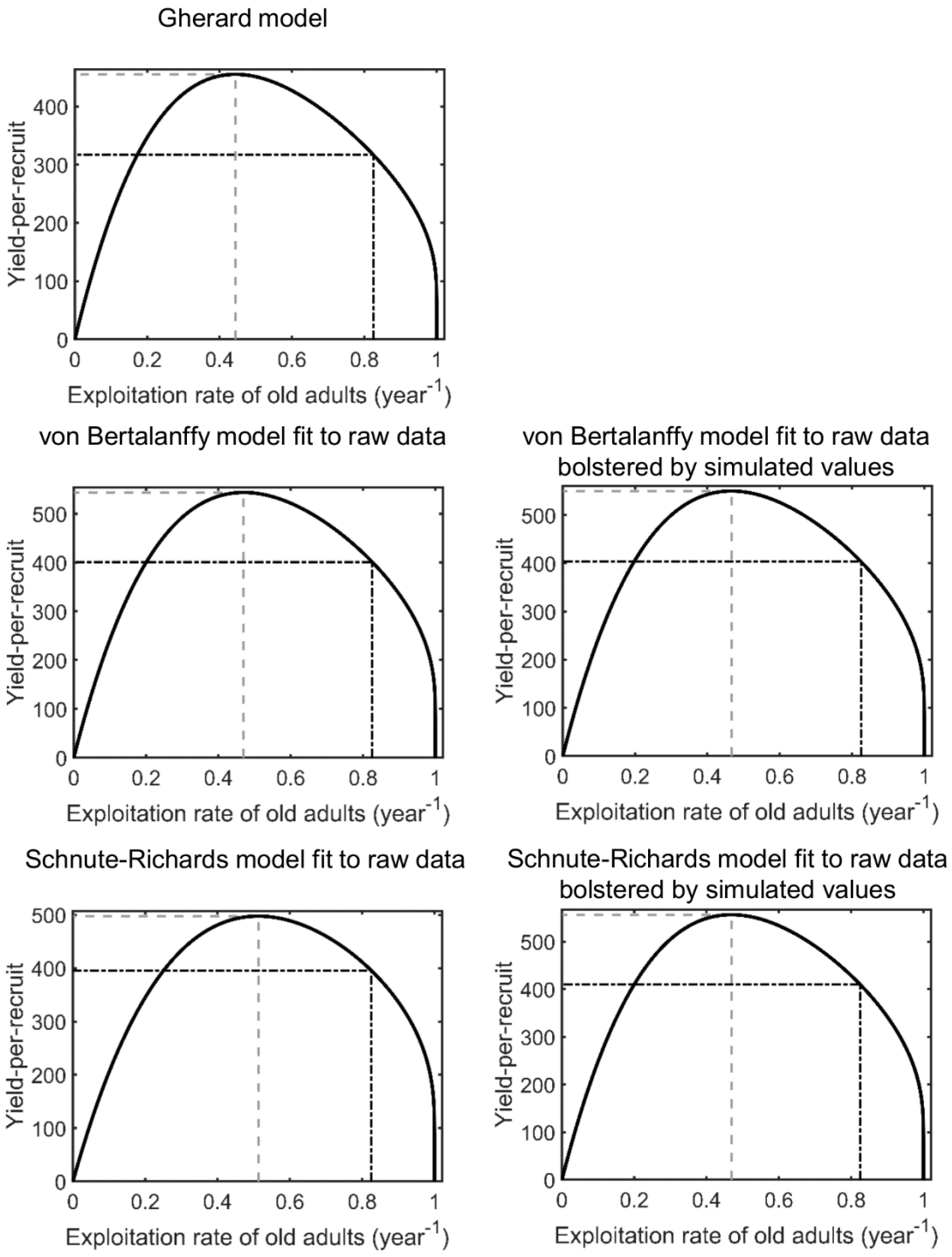

Figure S3. Yield-per-recruit models employing different growth models for Gulf Corvina

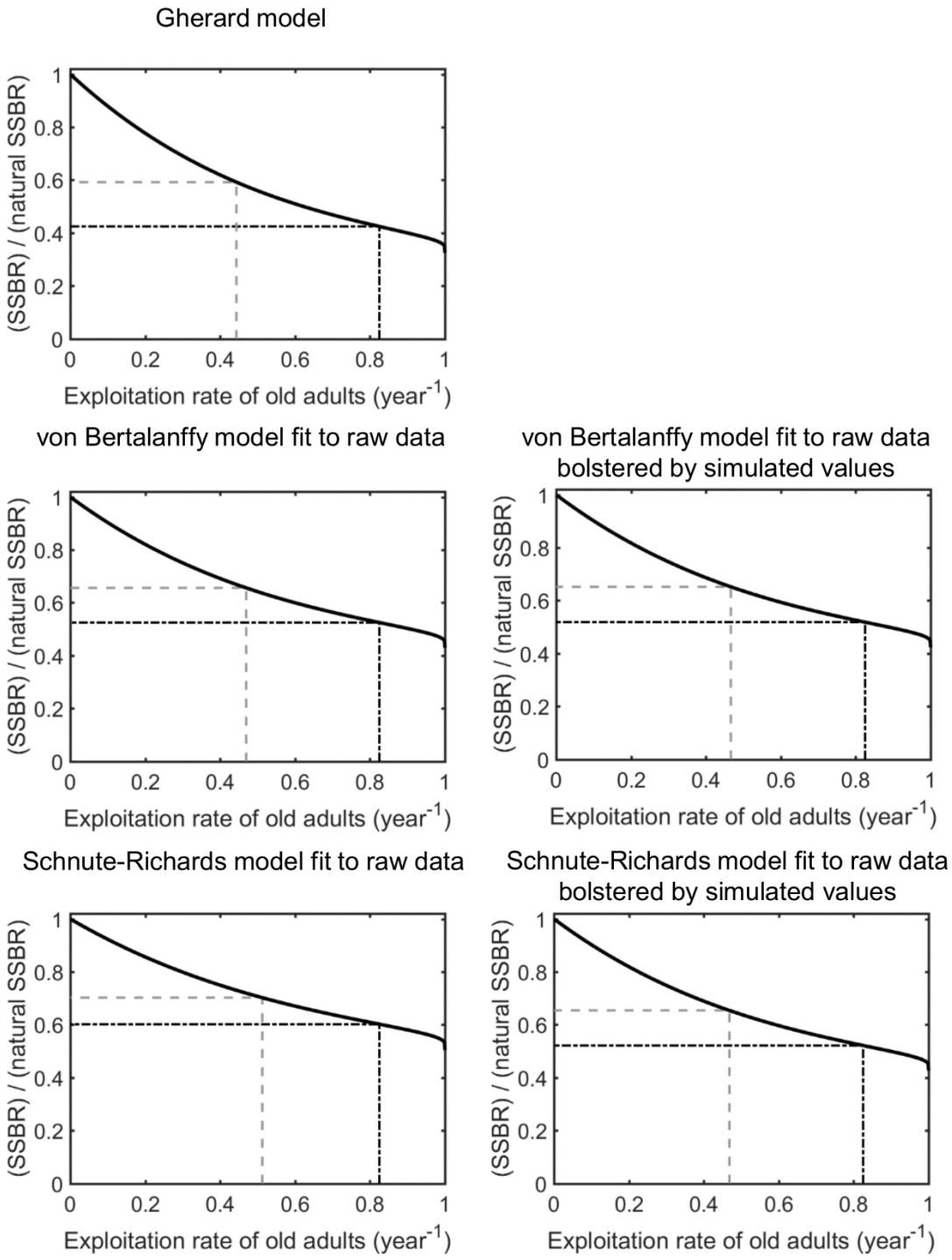

Figure S4. Spawning stock biomass-per-recruit employing different growth models for Gulf Corvina

References of Appendix 1.1

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Walsh, P., Grant, S., Winger, P., Blackwood, G., Balmori-Ramirez, A., Silva-Ramírez, T., 2004. An investigation of alternative harvesting methods to reduce the by-catch of Vaquita porpoise in the Upper Gulf of California shrimp gillnet fishery. Unpublished report prepared for World Wildlife Fund–US, Washington, DC.

Appendix S1.2. 95% confidence intervals for the growth parameters estimated from raw data.

The 95% confidence intervals for the von Bertalanffy, Gompertz, logistic, Schnute-Richards, and Schnute model growth parameters estimated from raw data are provided in Table S1, S2, S3, S4 and S4, respectively.

Table S1. Growth parameter estimates for the von Bertalanffy model fit to raw data

Parameter	Estimate	95% lower CI	95% upper CI
L_∞	916.048	858.953	989.574
K	0.281	0.233	0.333
t_0	-0.170	-0.365	-0.009

Table S2. Growth parameter estimates for the Gompertz model fit to raw data

Parameter	Estimate	95% lower CI	95% upper CI
L_∞	820.639	793.079	859.285
K	0.512	0.451	0.571
t_0	1.293	1.206	1.402

Table S3. Growth parameter estimates for the Schnute-Richards model fit to raw data

Parameter	Estimate	95% lower CI	95% upper CI
L_∞	778.880	758.583	802.346
K	0.757	0.688	0.833
t_0	1.918	1.828	2.024

Table S4. Growth parameter estimates for the Schnute model fit to raw data

Parameter	**Estimate**	**95% lower CI**	**95% upper CI**
a	3.356	2.761	4.277
b	-0.325	-0.479	-0.216

APPENDIX 2: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

Appendix 2.1. Results of generalized additive mixed modelling for each of the study species for which it was possible to develop models.

For all horizontal distribution binomial generalized additive mixed models (GAMMs), η is the probability of encounter of the species; g is a logit link function between η and each predictor; $t2(X,Y)$ is a tensor product smooth fitted to eastings and northings (i.e. longitude and latitude both expressed in Universal Transverse Mercator (UTM) coordinates); and visibility, platform and survey team are factors treated as random effects.

For all vertical distribution GAMMs, η is the probability of encounter; g is a logit link function between η and each predictor; $t2(X,Y)$ is a tensor product smooth fitted to eastings and northings; "depth bin within platforms" ($platform/depth\ bin$) is a nested random effect that accounts for the fact that different depth bins are surveyed within a given petroleum platform; and visibility and survey team are factors treated as random effects.

The list of parameters included in initial, full models and the range of values for those parameters may be found in Table 2 (horizontal distribution dataset) and Table 3 (vertical distribution dataset) in the manuscript.

S2.1.1: Atlantic Spadefish (*Chaetodipterus faber*)

Formula of the final vertical distribution binomial GAMM of Atlantic Spadefish (adjusted R^2: 0.246):

$$g(\eta) = t2(X,Y) + s(salinity) + visibility + (platform/depth\ bin) + survey\ team$$

(S2.1.1a)

S2.1.2: Bermuda Chub (*Kyphosus sectatrix*)

Formula of the final horizontal distribution GAMM of Bermuda Chub (adjusted R^2: 0.447):

$$g(\eta) = t2(X,Y) + s(salinity) + s(distance\ from\ shore) + visibility + platform + survey\ team$$

(S2.1.2a)

Formula of the final vertical distribution binomial GAMM of Bermuda Chub (adjusted R^2: 0.244):

$$g(\eta) = t2(X,Y) + s(salinity) + visibility + (platform/depth\ bin) + survey\ team$$

(S2.1.2b)

S2.1.3: Blue Runner (*Caranx crysos*)

Formula of the final horizontal distribution GAMM of Blue Runner (adjusted R^2: 0.286):

$$g(\eta) = t2(X,Y) + s(Number\ of\ platforms\ ) + visibility + platform + survey\ team$$

(S2.1.3a)

S2.1.4: Crevalle Jack (*Caranx hippos*)

Formula of the horizontal distribution final GAMM of Crevalle Jack (adjusted R^2: 0.252):

$$g(\eta) = t2(X,Y) + s(Number\ of\ platforms) + visibility + platform + survey\ team$$

(S2.1.4a)

S2.1.5: Greater Amberjack (*Seriola dumerili*)

Formula of the final horizontal distribution GAMM of Greater Amberjack (adjusted R^2: 0.662):

$$g(\eta) = t2(X,Y) + s(distance\ from\ shore) + visibility + platform + survey\ team$$

(S2.1.5a)

Formula of the final vertical distribution binomial GAMM of Greater Amberjack (adjusted R^2: 0.328):

$$g(\eta) = t2(X,Y) + s(dissolved\ oxygen) + s(salinity) + visibility + (platform/depth\ bin) + survey\ team$$

(S2.1.5b)

S2.1.6: Red Snapper (*Lutjanus campechanus*)

Formula of the final horizontal distribution GAMM of Red Snapper (adjusted R^2: 0.655):

$$g(\eta) = t2(X, Y) + s(dissolved\ oxygen) + s(salinity) + visibility + platform + survey\ team$$

(S2.1.6a)

Formula of the final vertical distribution binomial GAMM of Red Snapper (adjusted R^2: 0.271):

$$g(\eta) = t2(X, Y) + s(seafloor\ depth) + s(dissolved\ oxygen) + s(salinity) + visibility + (platform/depth\ bin) + survey\ team$$

(S2.1.6b)

S2.1.7: Vermilion Snapper (*Rhomboplites aurorubens*)

Formula of the final horizontal distribution GAMM of Vermilion Snapper (adjusted R^2: 0.338):

$$g(\eta) = t2(X, Y) + s(distance\ from\ shore) + visibility + platform + survey\ team$$

(S2.1.7a)

Formula of the final vertical distribution binomial GAMM of Vermilion Snapper (adjusted R^2: 0.139):

$$g(\eta) = t2(X, Y) + s(salinity) + visibility + (platform/depth\ bin) + survey\ team$$

(S2.1.7b)

Appendix 2.2. Correlation matricies for candidate continuous predictors in horizontal and vertical distribution generalized additive mixed models

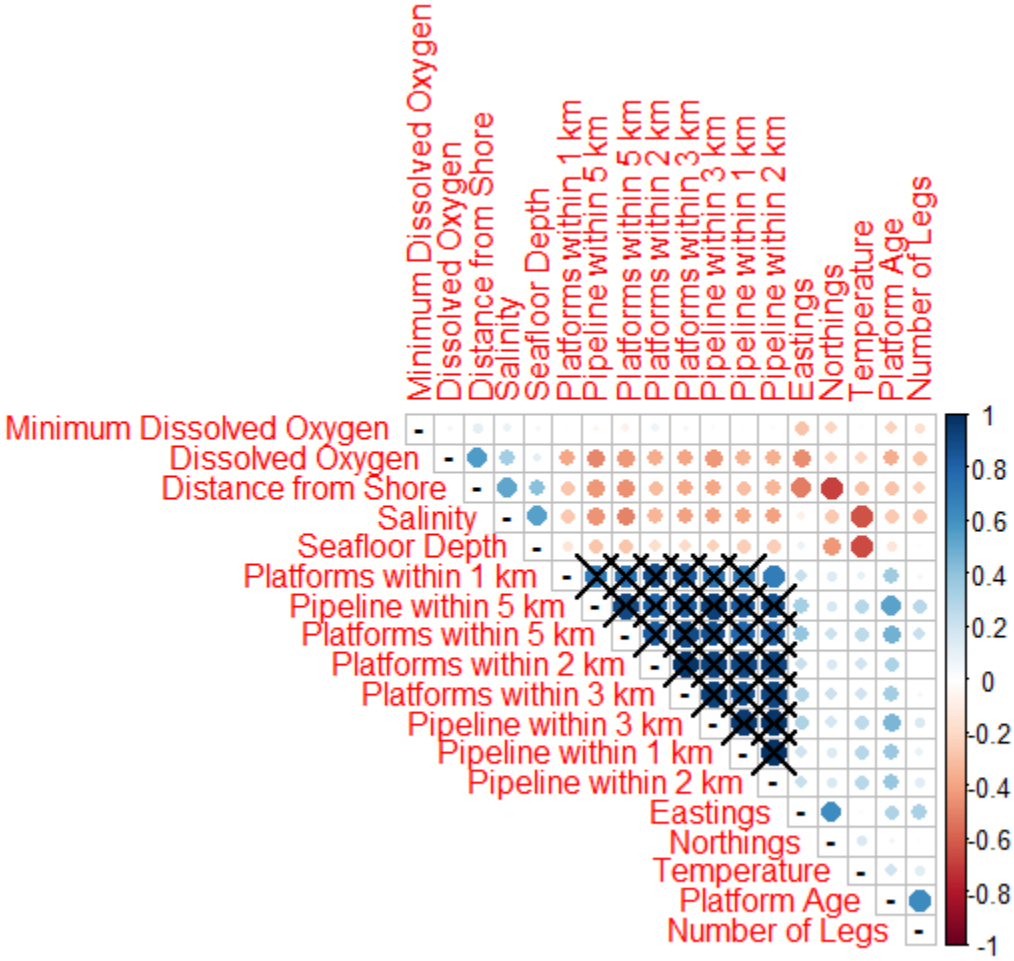


Fig. S2.2.1. Pearson correlation matrix for candidate continuous predictors of horizontal distribution GAMMs. The color of the circle within the grid represents the degree to which the correlation was positive or negative, and the size of the circle within the grid represents

the strength of the correlation, with "X" denoting correlations stronger than 0.7 in absolute value.

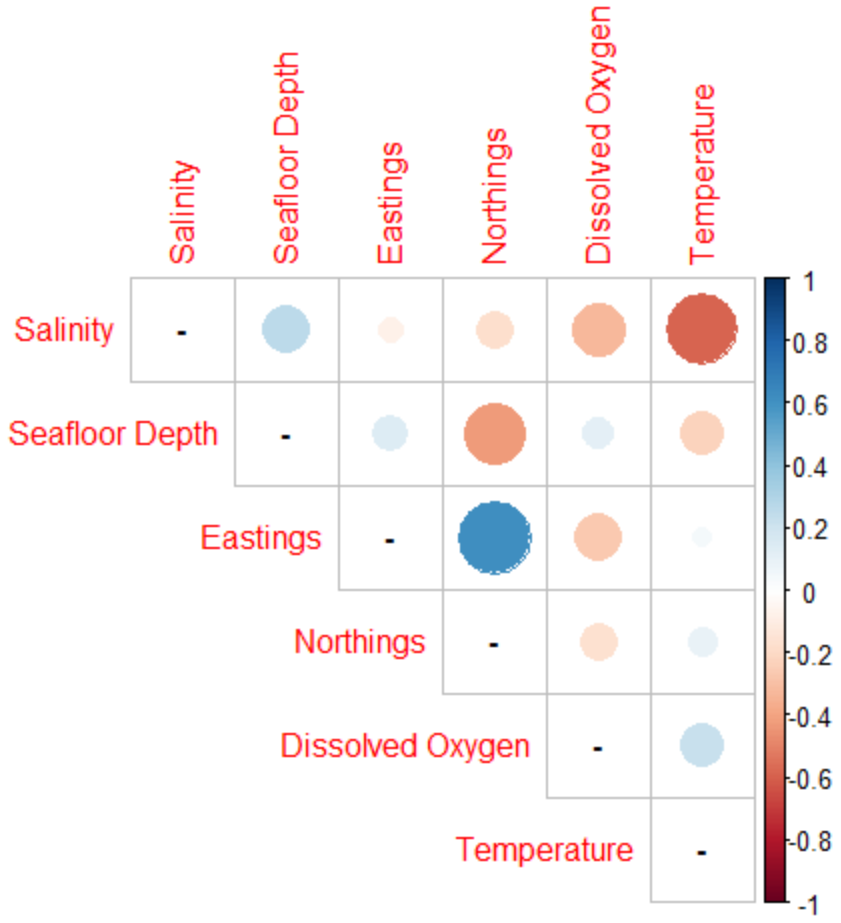


Fig. S2.2.2 Pearson correlation matrix for candidate continuous predictors of the vertical distribution GAMMs. The color of the circle within the grid represents the degree to which the correlation was positive or negative, and the size of the circle within the grid represents

the strength of the correlation**,** with "X" denoting correlations stronger than 0.7 in absolute value.

Appendix 2.3. Water column temperature and salinity measurements

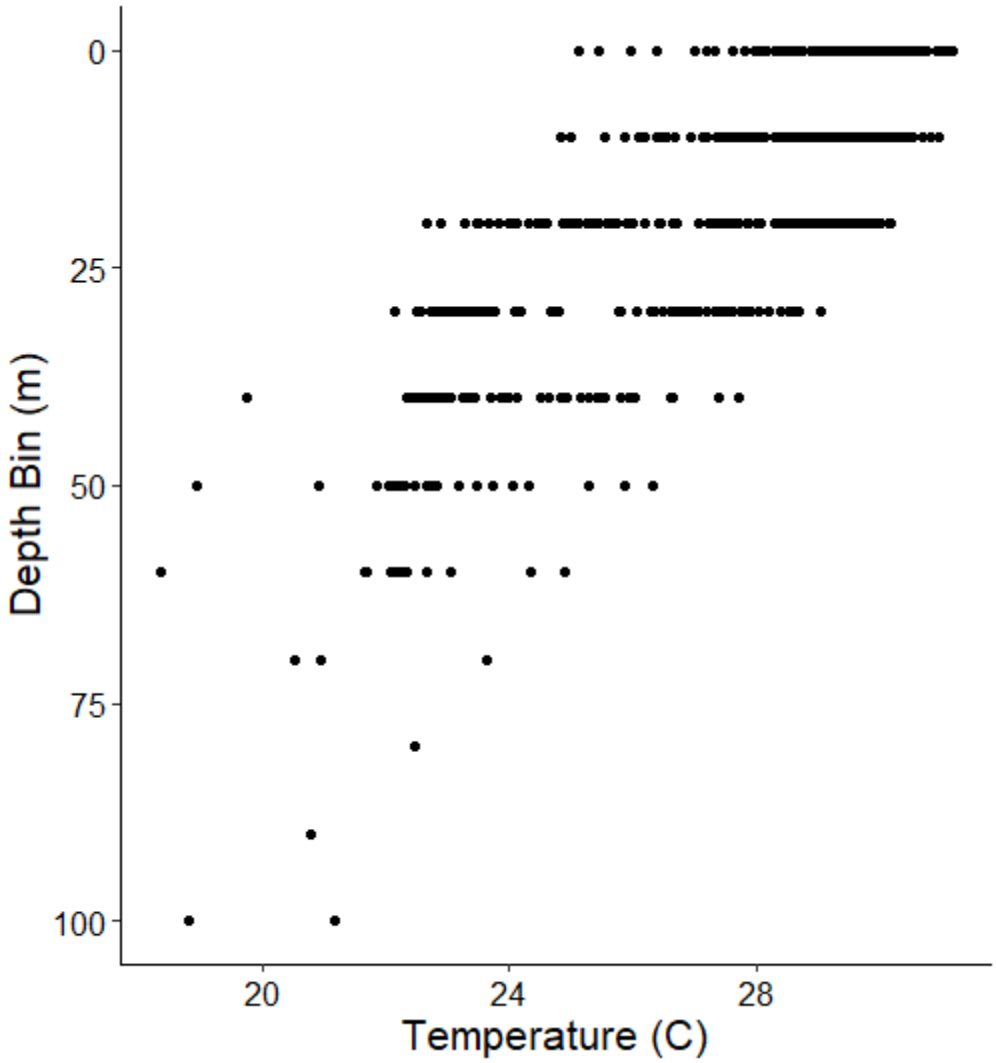


Fig. S2.3.1. Water column temperature measurements for each depth layer sampled at every site.

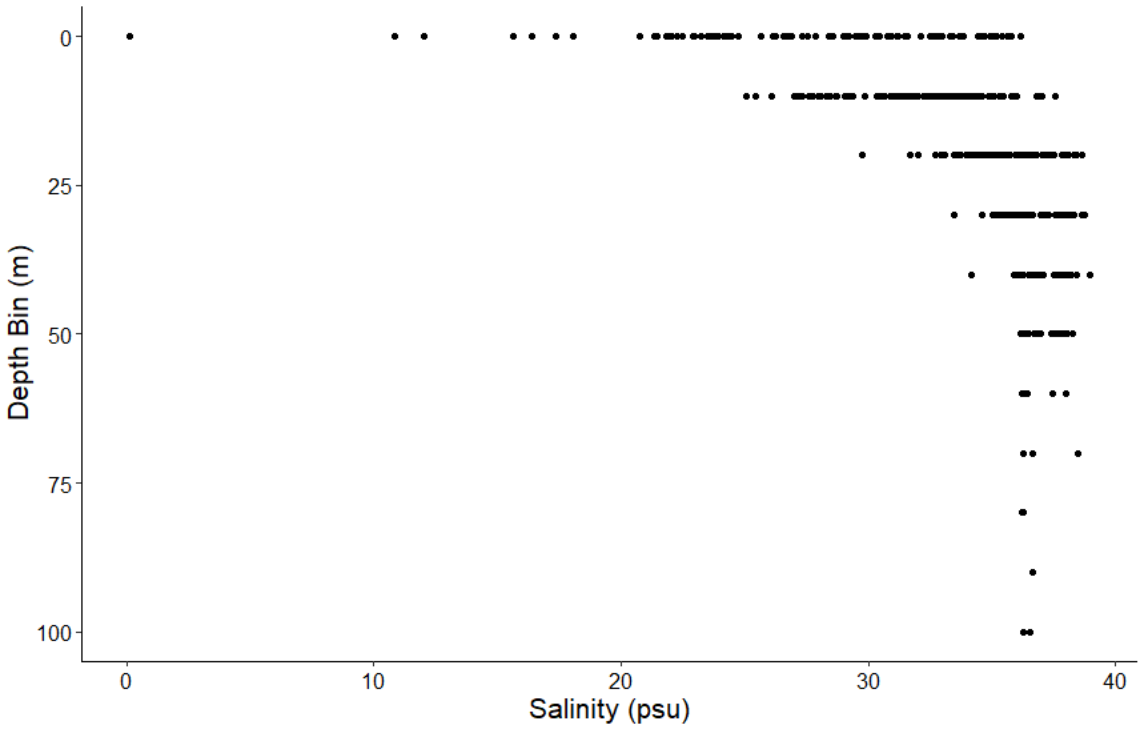


Fig. S2.3.2. Water column salinity measurements for each depth layer sampled at every site.

APPENDIX 3: SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table S3.1. Fishes observed but excluded from analyses.

Analysis	Species
Optic-Acoustic Estimates of Abundance	Blacktip Shark (*Carcharhinus limbatus*), Blue Angelfish (*Holacanthus bermudensis*), Bull Shark (*Carcharhinus leucas*), Carcharhinidae spp., Holicanthidae spp., Monocanthidae spp., Remora (*Remora* spp.), Sergeant Major (*Abudefduf saxatilis*), Spanish Hogfish (*Bodianus rufus*), Spotfin Butterflyfish (*Chaetodon ocellatus*), Queen Angelfish (*Holacanthus ciliaris*)
Community Analyses (Diversity, Richness, NMDS)	Blacktip Shark, Blue Angelfish, Bull Shark, Carangidae spp., Carcharhinidae spp., French Angelfish (*Pomacanthus paru*), Holicanthidae spp., Lutjanidae spp., Monocanthidae spp., Pomacanthidae spp., Red Porgy (*Pagrus pagrus*), Remora, Sergeant Major, Spanish Hogfish, Sphyridae spp., Spotfin Butterflyfish, Queen Angelfish

Table S3.2. Summary statistics for optic-acoustic abundance within 100 m of platform structure for all species considered in our analyses. Good visibility is defined as an average visibility score greater than 2.0/3.0.

Species	Average Abundance (good visibility)	Average Abundance (all sites)	Median Abundance (good visibility)	Median Abundance (all sites)	Standard Deviation of Abundance (good visibility)	Standard Deviation of Abundance (all sites)
Atlantic Bumper (*Chloroscombrus chrysurus*)	11,778	4,749	0	0	22,662	14,161
Blue Runner (*Caranx crysos*)	6,869	8,959	2,549	3,405	8,750	14,056
Bermuda Chub (*Kyphosus sectatrix*)	4,194	1,673	817	14	8,839	5,446
Red Snapper (*Lutjanus campechanus*)	3,871	2,347	3,353	1,902	2,971	2,489

Greater Amberjack (*Seriola dumerili*)	2,243	1,566	419	0	7,308	5,965
Crevalle Jack (*Caranx hippos*)	2,121	1,484	134	41	6,831	5,702
Vermilion Snapper (*Rhomboplites aurorubens*)	1,190	964	0	0	2,169	3,184
Atlantic Moonfish (*Selene setapinnis*)	864	304	0	0	3,638	2,121
Atlantic Spadefish (*Chaetodipterus faber*)	751	3,383	0	261	1,391	16,124
Guachanche Barracuda	660	224	0	0	2,330	1,370

(*Sphyraena guachancho*)						
Gray Snapper (*Lutjanus griseus*)	655	516	30	0	1,313	1,253
Horse-Eye Jack (*Caranx latus*)	576	217	0	0	1,913	1,130
Rainbow Runner (*Elagatis bipinnulata*)	553	270	0	0	2,296	1,410
Almaco Jack (*Seriola rivoliana*)	289	383	7	0	688	1,840
Bluefish (*Pomatomus saltatrix*)	192	65	0	0	837	488
Great Barracuda (*Sphyraena barracuda*)	172	115	34	0	383	272
Ocean Triggerfish	121	44	0	0	272	166

(*Canthidermis sufflamen*)						
Lookdown Jack (*Selene vomer*)	66	797	0	0	251	3,763
Gray Triggerfish (*Balistes capriscus*)	66	51	0	0	138	137
Cobia (*Rachycentron canadum*)	64	29	0	0	148	94
Grouper (*Epinephelinae spp.*)	34	22	0	0	98	94
King Mackerel (*Scomberomorus cavalla*)	26	19	0	0	88	66
Red Drum (*Sciaenops ocellatus*)	14	5	0	0	62	36

Sheepshead (*Archosargus probatocephalus*)	7	7	0	0	32	37
Yellow Jack (*Carangoides bartholomaei*)	6	8	0	0	16	50
Bar Jack (*Carangoides ruber*)	5	2	0	0	23	14
Dog Snapper (*Lutjanus jocu*)	5	2	0	0	22	13

Table S3.3. Percentage of sites with good water column visibility (average visibility score > 2.0/3.0) that each species observed was encountered at. These data from all sites can be found in Bolser et al. 2020.

Species	Percentage of sites
Bermuda Chub (*Kyphosus sectatrix*)	94.7
Red Snapper (*Lutjanus campechanus*)	94.7
Blue Runner (*Caranx crysos*)	79.0
Crevalle Jack (*Caranx hippos*)	73.7
Greater Amberjack (*Seriola dumerili*)	73.7

Gray Snapper (*Lutjanus griseus*)	57.9
Almaco Jack (*Seriola rivoliana*)	52.6
Great Barracuda (*Sphyraena barracuda*)	52.6
Atlantic Spadefish (*Chaetodipterus faber*)	47.4
Cobia (*Rachycentron canadium*)	36.8
Vermilion Snapper (*Rhomboplites aurorubens*)	36.8
Atlantic Bumper (*Chloroscombrus chrysurus*)	31.6
Ocean Triggerfish (*Canthidermis sufflamen*)	26.3
Rainbow Runner (*Elegatis bipinnulata*)	26.3
Gray Triggerfish (*Balistes capriscus*)	21.0
Grouper (non-specific)	21.0
Horse-Eye Jack (*Caranx latus*)	15.8
Yellow Jack (*Carangoides bartholomaei*)	15.8
Guachanche Barracuda (*Sphyraena guachancho*)	10.5
King Mackerel (*Scomberomorus cavalla*)	10.5
Lookdown Jack (*Selene vomer*)	10.5
Atlantic Moonfish (*Selene setapinnis*)	10.5
Bar Jack (*Caranx ruber*)	5.3

Bluefish (*Pomatomus saltatrix*)	5.3
Dog Snapper (*Lutjanus jocu*)	5.3
Red Drum (*Sciaenops ocellatus*)	5.3
Sheepshead (*Archosargus probatocephalus*)	5.3

Table S3.4. Variables that were not correlated with one another, or with eastings and northings, at a level less than 0.7 in absolute value, and, thus, were included in initial multiple-predictor GAMMs of species richness and diversity. DO = dissolved oxygen. This same suite of variables was included in the initial models of Bolser et al. (2020) and Egerton et al. (2021), except for distance to natural hard-bottom habitat. Egerton et al. (2021) also included turbidity in initial models. These variables were also considered individually in single-predictor models of the distribution and abundance of Greater Amberjack (*Seriola dumerili*), Red Snapper (*Lutjanus campechanus*) and Vermilion Snapper (*Rhomboplites aurorubens*) in the present study.

Analysis	Parameters considered
Species Richness, H' Diversity	DO concentration, salinity, temperature, minimum DO concentration, platform age, seafloor depth, distance from shore, distance to nearest hard-bottom habitat, number of legs, and number of platforms within 5 km of the study platform

Table S3.5. Significant results ($p < 0.05$, estimated degrees of freedom > 0.9, Adjusted-$R^2 > 0.1$) of Negative Binomial Generalized Additive Mixed Models of the abundance of Greater Amberjack (*Seriola dumerili*), Red Snapper (*Lutjanus campechanus*) and Vermilion Snapper (*Rhomboplites aurorubens*) from all sites. These models were fit in the same stepwise manner as described for the models of species richness and diversity in the main text. Site and visibility score were included as random effects as this dataset was not screened for visibility and it contained repeated site visits. Limited degrees of freedom precluded the inclusion of a tensor term between eastings and northings in these models.

Species	Parameter	*p*-value	EDF	Adjusted-R^2
Red Snapper	Distance from Shore (km)	<0.001*	2.62	0.40

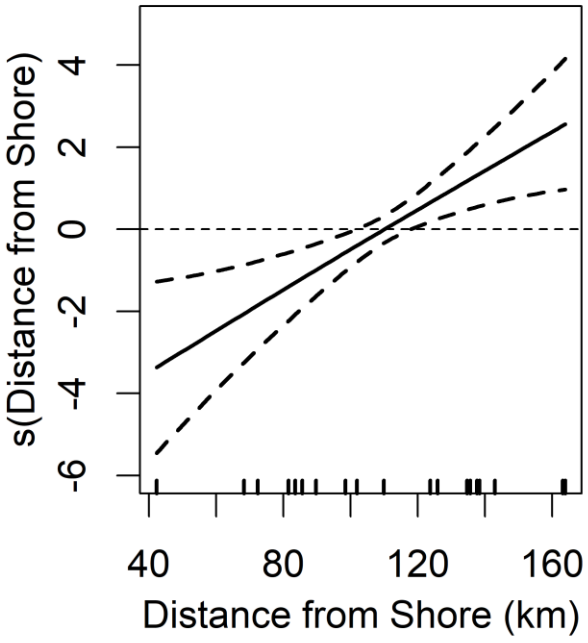


Figure S3.1. Marginal effect of distance from shore on Greater Amberjack (*Seriola dumerili*) abundance from sites with good visibility (average visibility score > 2.0/3.0).

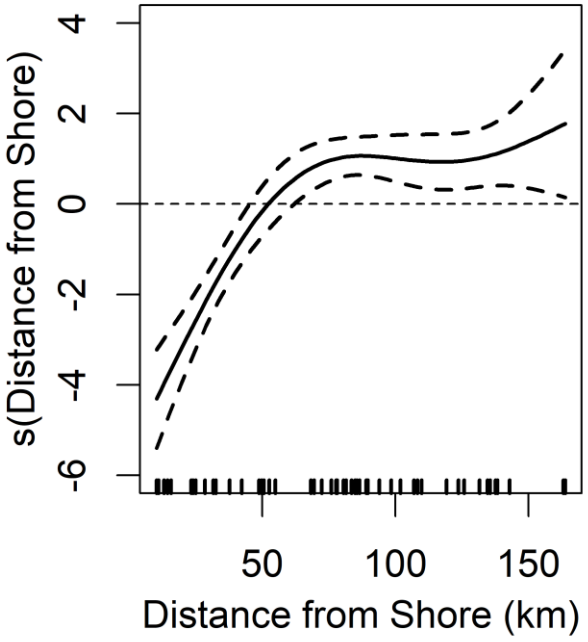


Figure S3.2. Marginal effect of distance from shore on Red Snapper (*Lutjanus campechanus*) abundance from all sites.

APPENDIX 4: SUPPLEMENTARY MATERIAL FOR CHAPTER 5

Appendix 4.1. Detailed statistics for the full dataset in table-form

Table S4.1.1. Average orientation angle of all tracked fishes. Values are means, with standard deviations in parentheses.

Average orientation angle	Average absolute orientation angle
0.27º (*15.55*º)	10.40º (*11.57*º)

Table S4.1.2. Results of Gamma Generalized Linear Models describing the effect of fish orientation angle and absolute angle on σbs (linearized target strength). Despite significant *p*-values, the low adjusted-R^2 values indicate that orientation angle and absolute orientation angle do not have an effect on σbs in our dataset.

	Angle	Absolute angle
Adjusted-R^2	2.87 e^{-5}	2.85 e^{-3}
p-value	<0.01*	< 0.001*

Table S4.1.3. Results of Gamma Generalized Linear Models (GLMs) describing the effect of average fish orientation angle and absolute angle on size spectrum slopes. GLMs were fit to the absolute value of size spectrum slope

	Slope from general TS-length model data vs. angle	Slope from general TS-length model data vs. absolute angle	Slope from specific TS-length model data vs. angle	Slope from specific TS-length model data vs. absolute angle
Adjusted-R^2	0.03	0.01	0.01	0.01
p-value	0.09	0.10	0.20	0.06

Table S4.1.4. Average coefficient of variation (CV) from the analysis of fish orientation's effect on size spectrum slope. Note that these CVs were calculated from 49 of the 51 sites included in Chapter 5 due to computational constraints.

General TS-length model dataset mean CV	Specific TS-length model dataset mean CV
0.6%	0.8%

Table S4.1.5. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean size spectrum slope between datasets. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	Unadjusted *p*-value	Adjusted *p*-value
Sim. all fish - Sim. small fish	0.92088	0.357113	1
Sim. all fish - Expected	-1.05369	0.292025	1
Sim. small fish - Expected	-1.97457	0.048317*	0.531487114
Sim. all fish - General TS-length	6.280427	3.38E-10*	5.74E-09*
Sim. small fish - General TS-length	5.359546	8.34E-08*	1.25E-06*
Expected - General TS-length	7.334116	2.23E-13*	4.69E-12*
Sim. all fish - Community census	-0.92538	0.354766	1
Sim. small fish - Community census	-1.34791	0.177686	1
Expected - Community census	-0.44192	0.658549	1
General TS-length - Community census	-3.80704	0.000141*	0.001828313*
Sim. all fish - Sim. large fish	-0.99552	0.319485	1
Sim. small fish - Sim. large fish	-1.9164	0.055315	0.553145583
Expected - Sim. large fish	0.058172	0.953611	0.953611287
General TS-length - Sim. large fish	-7.27594	3.44E-13*	6.88E-12*
Community census - Sim. large fish	0.468609	0.639349	1

Sim. all fish - Specific TS-length	5.919318	3.23E-09*	5.17E-08*
Sim. small fish - Specific TS-length	4.998438	5.78E-07*	8.09E-06*
Expected - Specific TS-length	6.973008	3.10E-12*	5.89E-11*
General TS-length - Specific TS-length	-0.36111	0.718019	1
Community census - Specific TS-length	3.641353	0.000271*	0.003254505*
Sim. large fish - Specific TS-length	6.914835	4.68E-12*	8.43E-11*

Table S4.1.6. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean fish length between datasets. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	17.94592	5.16E-72*	2.07E-71*
Sim. all fish - Expected	-319.152	0*	0*
Sim. small fish - Expected	-457.054	0*	0*
Sim. all fish - General TS-length	785.5728	0*	0*
Sim. small fish - General TS-length	1028.06	0*	0*
Expected - General TS-length	2464.113	0*	0*
Sim. all fish - Community census	-74.5249	0*	0*
Sim. small fish - Community census	-78.8991	0*	0*
Expected - Community census	-16.7714	3.95E-63*	1.19E-62*
General TS-length - Community census	-220.125	0*	0*
Sim. all fish - Sim. large fish	13.80807	2.28E-43*	4.56E-43*
Sim. small fish - Sim. large fish	2.289274	0.022063*	0.0220638
Expected - Sim. large fish	222.3675	0*	0*

General TS-length - Sim. large fish	-492.083	0*	0*
Community census - Sim. large fish	77.25179	0*	0*
Sim. all fish - Specific TS-length	551.4644	0*	0*
Sim. small fish - Specific TS-length	713.1739	0*	0*
Expected - Specific TS-length	1939.62	0*	0*
General TS-length - Specific TS-length	-521.565	0*	0*
Community census - Specific TS-length	177.0598	0*	0*
Sim. large fish - Specific TS-length	340.7439	0*	0*

Appendix 4.2. Comparisons between full and reduced datasets

Table S4.2.1. Median (standard deviation in parentheses) size spectrum slope for each dataset. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. full TS range" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small pelagic TS" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large piscivore TS" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Data type	Community census	Expected	Specific TS-length conversion	General TS-length conversion	Simulation: full TS range	Simulation: small pelagic TS	Simulation: large piscivore TS
All data	-1.31 (0.21)	-1.29 (0.90)	-2.59 (1.12)	-2.33 (0.88)	-1.38 (0.48)	-1.48 (0.45)	-1.24 (0.57)
Visibility & angle filtered	-1.31 (0.21)	-1.68 (0.66)	-2.65 (1.19)	-2.58 (0.72)	-1.51 (0.57)	-1.55 (0.43)	-1.31 (0.71)
Visibility filtered	-1.31 (0.21)	-1.65 (0.61)	-2.59 (1.22)	-2.31 (0.83)	-1.38 (0.60)	-1.49 (0.49)	-1.24 (0.67)

Angle filtered	-1.31 (0.21)	-1.51 (0.71)	-2.65 (1.00)	-2.46 (0.80)	-1.48 (0.51)	-1.50 (0.38)	-1.31 (0.69)

Table S4.2.2. Median (standard deviation in parentheses) fish total length (cm) in each dataset. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. full TS range" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small pelagic TS" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large piscivore TS" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Data type	Community census	Expected	Specific TS-length conversion	General TS-length conversion	Simulation: full TS range	Simulation: small pelagic TS	Simulation: large piscivore TS
All data	32.50 (*10.83*)	27.87 (*15.71*)	4.74 (6.03)	3.48 (4.66)	14.80 (16.60)	14.80 (9.79)	13.31 (33.02)
Visibility & angle filtered	32.50 (*10.83*)	20.11 (24.84)	5.31 (8.20)	4.38 (5.82)	12.81 (16.10)	12.81 (10.92)	8.38 (25.37)
Visibility filtered	32.50 (*10.83*)	20.90 (24.13)	5.60 (8.52)	5.00 (6.39)	12.81 (16.39)	12.81 (11.33)	9.25 (24.96)
Angle filtered	32.50 (*10.83*)	28.17 (15.43)	4.74 (5.34)	3.48 (4.14)	14.80 (16.38)	14.80 (9.15)	10.89 (35.43)

Table. S4.2.3. Kruskal-Wallis (KW) test results for testing differences in fish length between datasets

Data type	KW χ^2	Degrees of freedom	*p*-value
All data	7,107,693	6	$< 2.2e^{-16}$*

Visibility & angle filtered	1,385,162	6	$< 2.2e^{-16}$*
Visibility filtered	1,578,320	6	$< 2.2e^{-16}$*
Angle filtered	6,183,630	6	$< 2.2e^{-16}$*

Table S4.2.4. Kruskal-Wallis (KW) test results for testing differences in size spectrum slope between the fish collection, expected, general TS-length, and specific TS-length datasets

Data type	KW χ^2	Degrees of freedom	*p*-value
All data	117.45	6	$2.2e^{-16}$*
Visibility & angle filtered	28.51	6	$7.53e^{-5}$*
Visibility filtered	29.01	6	$6.05e^{-5}$*
Angle filtered	64.90	6	$4.51e^{-12}$*

Supplementary material S3. Detailed statistics for the datasets reduced by visibility and orientation thresholds.

Table S4.3.1. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean size spectrum slope between datasets. For this analysis, surveys with visibility scores > 2.0/3.0 were excluded, as were surveys in with average fish orientation > 2.0º and < -2.0º. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	0.256265	0.797746	1
Sim. all fish - Expected	-0.22132	0.824844	0.824844
Sim. small fish - Expected	-0.47758	0.632946	1
Sim. all fish - General TS-length	2.935397	0.003331*	0.053299
Sim. small fish - General TS-length	2.679132	0.007381*	0.103339
Expected - General TS-length	3.156716	0.001596*	0.02872*
Sim. all fish - Community census	-1.26434	0.206108	1
Sim. small fish - Community census	-1.48627	0.137208	1
Expected - Community census	-1.07267	0.283419	1
General TS-length - Community census	-3.80647	0.000141*	0.00296*
Sim. all fish - Sim. large fish	-0.55912	0.576078	1
Sim. small fish - Sim. large fish	-0.81539	0.41485	1
Expected - Sim. large fish	-0.3378	0.735511	1
General TS-length - Sim. large fish	-3.49452	0.000475*	0.009498*
Community census - Sim. large fish	0.780124	0.435318	1
Sim. all fish - Specific TS-length	2.539351	0.011106*	0.144376
Sim. small fish - Specific TS-length	2.283086	0.022425*	0.269103
Expected - Specific TS-length	2.760671	0.005768*	0.086524
General TS-length - Specific TS-length	-0.39605	0.692071	1
Community census - Specific TS-length	3.463481	0.000533*	0.010131*
Sim. large fish - Specific TS-length	3.098474	0.001945*	0.033068*

Table S4.3.2. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean fish length between datasets. For this analysis, surveys with visibility scores > 2.0/3.0 were excluded, as were surveys in with average fish orientation > 2.0º and < -2.0º. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated

using the expected TS of small planktivorous fishes and specific TS-length models were used; “Sim. large fish” refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	-11.8239	2.94E-32*	2.94E-32*
Sim. all fish - Expected	-202.614	0*	0*
Sim. small fish - Expected	-240.746	0*	0*
Sim. all fish - General TS-length	354.0694	0*	0*
Sim. small fish - General TS-length	468.5902	0*	0*
Expected - General TS-length	1077.107	0*	0*
Sim. all fish - Community census	-91.5805	0*	0*
Sim. small fish - Community census	-88.9275	0*	0*
Expected - Community census	-25.6144	1.05E-144*	2.11E-144*
General TS-length - Community census	-217.68	0*	0*
Sim. all fish - Sim. large fish	30.15913	8.14E-200*	2.44E-199*
Sim. small fish - Sim. large fish	41.92162	0*	0*
Expected - Sim. large fish	184.2213	0*	0*
General TS-length - Sim. large fish	-224.162	0*	0*
Community census - Sim. large fish	102.9165	0*	0*
Sim. all fish - Specific TS-length	247.6141	0*	0*
Sim. small fish - Specific TS-length	332.7888	0*	0*
Expected - Specific TS-length	868.9555	0*	0*
General TS-length - Specific TS-length	-204.539	0*	0*
Community census - Specific TS-length	180.9902	0*	0*
Sim. large fish - Specific TS-length	146.1385	0*	0*

Table S4.3.3. Mann-Whitney-Wilcoxon rank sum test results for differences in mean size spectrum slope between full and reduced datasets. For this analysis, surveys with visibility scores > 2.0/3.0 and average fish orientation between 2.0º and -2.0º were compared with the full datasets. “Expected” refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.’s (2001) fish collections and FishBase (Froese and Pauly 2020), “General TS-length model” refers to data from size distributions generated using Love’s (1971) general target strength (TS) to length model; and “Specific TS-length model” refers to data from size distributions based on specific TS-length models for species or groups of species; “All fish around schools simulation” refers to data in which TS for

single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; “Small fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; “Large fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Dataset	W	*p*-value
Expected	199.5	0.28
General TS-length model	214.0	0.43
Specific TS-length model	237.5	0.74
All fish around schools simulation	205.5	0.34
Small fish around schools simulation	195.5	0.25
Large fish around schools simulation	235.5	0.71

Table S4.3.4. Mann-Whitney-Wilcoxon rank sum test results for differences in mean fish length between full and reduced datasets. For this analysis, surveys with visibility scores > 2.0/3.0 and average fish orientation between 2.0º and -2.0º were compared with the full datasets. “Expected” refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.’s (2001) fish collections and FishBase (Froese and Pauly 2020), “General TS-length model” refers to data from size distributions generated using Love’s (1971) general target strength (TS) to length model; and “Specific TS-length model” refers to data from size distributions based on specific TS-length models for species or groups of species; “All fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; “Small fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; “Large fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used. Significant *p*-values were likely an artifact of very large sample sizes, as differences between mean lengths were not substantial (Table S4.2.2).

Dataset	W	*p*-value

Expected	872,666,160,101	< 0.0001*
General TS-length model	1,041,600,161,267	< 0.0001*
Specific TS-length model	800,853,538,430	< 0.0001*
All fish around schools simulation	15,742,404,454	< 0.0001*
Small fish around schools simulation	56,592,722,657	< 0.0001*
Large fish around schools simulation	3,004,940,466	< 0.0001*

Appendix 4.4. Detailed statistics for the datasets reduced by a visibility threshold

Table S4.4.1. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean size spectrum slope between datasets. Surveys with visibility scores > 2.0/3.0 were excluded for this analysis. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	0.410665	0.681318	1
Sim. all fish - Expected	0.865133	0.386966	1
Sim. small fish - Expected	0.454469	0.649491	1
Sim. all fish - General TS-length	3.471485	0.000518*	0.010352*
Sim. small fish - General TS-length	3.06082	0.002207*	0.037524*
Expected - General TS-length	2.606352	0.009151*	0.128117
Sim. all fish - Community census	-0.57876	0.562753	1
Sim. small fish - Community census	-0.87539	0.381364	1

Expected - Community census	-1.20366	0.228723	1
General TS-length - Community census	-3.08626	0.002027*	0.036484*
Sim. all fish - Sim. large fish	-0.52565	0.599131	1
Sim. small fish - Sim. large fish	-0.93632	0.349111	1
Expected - Sim. large fish	-1.39078	0.164291	1
General TS-length - Sim. large fish	-3.99714	6.41E-05*	0.001346*
Community census - Sim. large fish	0.199071	0.842207	0.842207
Sim. all fish - Specific TS-length	2.896555	0.003773*	0.060366
Sim. small fish - Specific TS-length	2.48589	0.012923*	0.167996
Expected - Specific TS-length	2.031421	0.042212*	0.506548
General TS-length - Specific TS-length	-0.57493	0.565338	1
Community census - Specific TS-length	2.670982	0.007563*	0.113445
Sim. large fish - Specific TS-length	3.422205	0.000621*	0.011802*

Table S4.4.2. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean fish length between datasets. Surveys with visibility scores > 2.0/3.0 were excluded from this analysis. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	-6.51083	7.47E-11*	7.47E-11*
Sim. all fish - Expected	-216.958	0*	0*
Sim. small fish - Expected	-264.483	0*	0*
Sim. all fish - General TS-length	397.1773	0*	0*

Sim. small fish - General TS-length	510.9286	0*	0*
Expected - General TS-length	1146.556	0*	0*
Sim. all fish - Community census	-88.8926	0*	0*
Sim. small fish - Community census	-88.1245	0*	0*
Expected - Community census	-24.4461	5.54E-132*	1.11E-131*
General TS-length - Community census	-215.483	0*	0*
Sim. all fish - Sim. large fish	25.63628	6.01E-145*	1.80E-144*
Sim. small fish - Sim. large fish	33.04713	1.71E-239*	6.84E-239*
Expected - Sim. large fish	194.5089	0*	0*
General TS-length - Sim. large fish	-270.053	0*	0*
Community census - Sim. large fish	97.73791	0*	0*
Sim. all fish - Specific TS-length	281.6804	0*	0*
Sim. small fish - Specific TS-length	364.9518	0*	0*
Expected - Specific TS-length	928.8654	0*	0*
General TS-length - Specific TS-length	-214.242	0*	0*
Community census - Specific TS-length	179.5995	0*	0*
Sim. large fish - Specific TS-length	182.7599	0*	0*

Table S4.4.3. Mann-Whitney-Wilcoxon rank sum test results for differences in mean size spectrum slope between full and reduced datasets. For this analysis, surveys with visibility scores > 2.0/3.0 were compared with the full datasets. “Expected” refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.’s (2001) fish collections and FishBase (Froese and Pauly 2020), “General TS-length model” refers to data from size distributions generated using Love’s (1971) general target strength (TS) to length model; and “Specific TS-length model” refers to data from size distributions based on specific TS-length models for species or groups of species; “All fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; “Small fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; “Large fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Dataset	W	*p*-value

Expected	566	0.06
General TS-length model	405	0.69
Specific TS-length model	383	0.48
All fish around schools simulation	411	0.76
Small fish around schools simulation	404	0.68
Large fish around schools simulation	413	0.78

Table S4.4.4. Mann-Whitney-Wilcoxon rank sum test results for differences in mean fish length between full and reduced datasets. For this analysis, surveys with visibility scores > 2.0/3.0 were compared with the full datasets. "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General TS-length model" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific TS-length model" refers to data from size distributions based on specific TS-length models for species or groups of species; "All fish around schools simulation" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Small fish around schools simulation" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Large fish around schools simulation" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Dataset	W	*p*-value
Expected	1,371,013,839,964	< 0.0001*
General TS-length model	1,151,368,813,610	< 0.0001*
Specific TS-length model	1,283,747,116,243	< 0.0001*
All fish around schools simulation	24,502,469,459	< 0.0001*
Small fish around schools simulation	86,065,510,731	< 0.0001*
Large fish around schools simulation	5,221,202,601	< 0.0001*

Appendix 4.5. Detailed statistics for the datasets filtered by an orientation angle threshold

Table S4.5.1. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean size spectrum slope between datasets. Surveys in which average fish orientation was > 2.0º or < -2.0º were excluded from this analysis. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	0.413873	0.678967	1
Sim. all fish - Expected	-0.65924	0.509741	1
Sim. small fish - Expected	-1.07311	0.28322	1
Sim. all fish - General TS-length	4.419574	9.89E-06*	0.000168*
Sim. small fish - General TS-length	4.0057	6.18E-05*	0.000804*
Expected - General TS-length	5.078814	3.80E-07*	7.98E-06*
Sim. all fish - Community census	-1.42774	0.153367	1
Sim. small fish - Community census	-1.68118	0.092728	1
Expected - Community census	-1.02404	0.305818	1
General TS-length - Community census	-4.13416	3.56E-05*	0.000534*
Sim. all fish - Sim. large fish	-0.62968	0.528905	1
Sim. small fish - Sim. large fish	-1.04355	0.296693	1
Expected - Sim. large fish	0.029562	0.976416	1
General TS-length - Sim. large fish	-5.04925	4.44E-07*	8.43E-06*
Community census - Sim. large fish	1.04214	0.297347	1
Sim. all fish - Specific TS-length	4.416617	1.00E-05*	0.00016*

Sim. small fish - Specific TS-length	4.002744	6.26E-05*	0.000751*
Expected - Specific TS-length	5.075858	3.86E-07*	7.72E-06*
General TS-length - Specific TS-length	-0.00296	0.997641	0.997641
Community census - Specific TS-length	4.132352	3.59E-05*	0.000503*
Sim. large fish - Specific TS-length	5.046296	4.50E-07*	8.11E-06*

Table S4.5.2. Dunn's Kruskal-Wallis multiple comparison *p*-values adjusted with the Holm method for differences in mean fish length between datasets. Surveys in which average fish orientation was > 2.0º or < -2.0º. "Community census" refers to data from Gitschlag et al.'s (2001) fish collections after explosive severance procedures were used to decommission petroleum platforms; "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific" refers to data from size distributions based on specific TS-length models for species or groups of species; "Sim. all fish" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Sim. small fish" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Sim. large fish" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Comparison	Z	P.unadj	P.adj
Sim. all fish - Sim. small fish	4.375556	1.21E-05*	1.21E-05*
Sim. all fish - Expected	-307.204	0*	0*
Sim. small fish - Expected	-423.286	0*	0*
Sim. all fish - General TS-length	701.547	0*	0*
Sim. small fish - General TS-length	943.8889	0*	0*
Expected - General TS-length	2306.074	0*	0*
Sim. all fish - Community census	-77.3613	0*	0*
Sim. small fish - Community census	-79.0997	0*	0*
Expected - Community census	-16.2812	1.34E-59*	2.68E-59*
General TS-length - Community census	-221.062	0*	0*
Sim. all fish - Sim. large fish	27.49796	1.86E-166*	7.43E-166*

Sim. small fish - Sim. large fish	26.57097	1.47E-155*	4.41E-155*
Expected - Sim. large fish	219.5751	0*	0*
General TS-length - Sim. large fish	-398.378	0*	0*
Community census - Sim. large fish	84.82504	0*	0*
Sim. all fish - Specific TS-length	484.6426	0*	0*
Sim. small fish - Specific TS-length	649.9763	0*	0*
Expected - Specific TS-length	1811	0*	0*
General TS-length - Specific TS-length	-495.914	0*	0*
Community census - Specific TS-length	177.0192	0*	0*
Sim. large fish - Specific TS-length	265.4825	0*	0*

Table S4.5.3. Mann-Whitney-Wilcoxon rank sum test results for differences in mean size spectrum slope between full and reduced datasets. For this analysis, surveys with average fish orientation between 2.0º and -2.0º were compared with the full datasets. “Expected” refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.’s (2001) fish collections and FishBase (Froese and Pauly 2020), “General TS-length model” refers to data from size distributions generated using Love’s (1971) general target strength (TS) to length model; and “Specific TS-length model” refers to data from size distributions based on specific TS-length models for species or groups of species; “All fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; “Small fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; “Large fish around schools simulation” refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used.

Dataset	W	*p*-value
Expected	583	0.39
General TS-length model	616	0.62
Specific TS-length model	609	0.56
All fish around schools simulation	557	0.26
Small fish around schools simulation	562	0.28
Large fish around schools simulation	615	0.61

Table S4.5.4. Mann-Whitney-Wilcoxon rank sum test results for differences in mean fish length between full and reduced datasets. For this analysis, surveys with average fish orientation between 2.0º and -2.0º were compared with the full datasets. "Expected" refers to data from expected size distributions at study sites based on the relative abundance of species and biological data from Gitschlag et al.'s (2001) fish collections and FishBase (Froese and Pauly 2020), "General TS-length model" refers to data from size distributions generated using Love's (1971) general target strength (TS) to length model; and "Specific TS-length model" refers to data from size distributions based on specific TS-length models for species or groups of species; "All fish around schools simulation" refers to data in which TS for single targets around schools was simulated using the expected TS of all fishes observed at platforms and specific TS-length models were used; "Small fish around schools simulation" refers to data in which TS for single targets around schools was simulated using the expected TS of small planktivorous fishes and specific TS-length models were used; "Large fish around schools simulation" refers to data in which TS for single targets around schools was simulated using the expected TS of large piscivorous fishes and specific TS-length models were used. Significant *p*-values were likely an artifact of very large sample sizes, as differences between mean lengths were not substantial (Table S4.2.2).

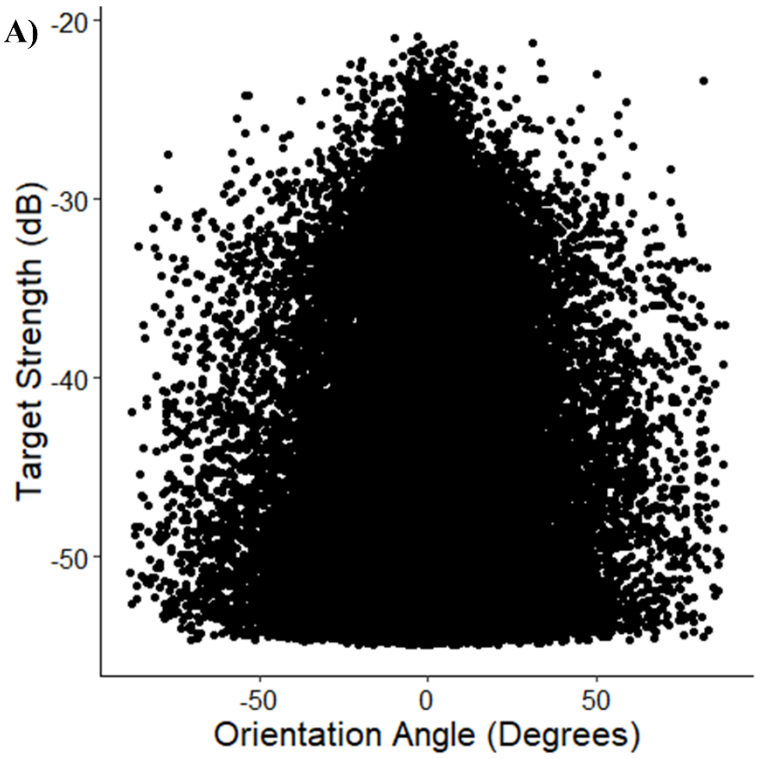
Dataset	W	*p*-value
Expected	4,287,988,198,071	< 0.0001*
General TS-length model	4,143,778,718,182	< 0.0001*
Specific TS-length model	4,304,078,437,860	< 0.0001*
All fish around schools simulation	49,080,366,133	< 0.0001*
Small fish around schools simulation	210,066,450,521	< 0.0001*
Large fish around schools simulation	6,641,496,852	< 0.0001*

Appendix 4.6. Alternative data used in the generation of simulated communities

Table S4.6.1. Alternative data used for biological parameters in simulated community generation when data were not available in Gitschlag et al. (2001) or FishBase (Froese and Pauly 2020). The data described in this table were all extracted from FishBase (Froese and Pauly 2020).

Species	Alternative data used
Brevoortia patronus	½ of the range of length at maturity used for the standard deviation of length
Oligoplites saurus	½ difference between common length and max length used for standard deviation of length
Serranidae spp.	Data were from *Mycteroperca phenax*. 2/3 of common length used as the lower bound of the truncated normal distribution
Selene vomer	½ difference between common length and max length used for standard deviation of length
Rhomboplites aurorubens	½ of the range of length at maturity used for the standard deviation of length
Canthidermis sufflamen	No data on FishBase except for max length; data from *Balistes capriscus* was used for all other biological parameters
Seriola dumerili	½ difference between common length and max length used for standard deviation of length. Common length minus the ½ difference between common and max length was used as the lower bound of the truncated normal distribution.

Supplementary Figures


A)
-20
-30
-40
-50
Target Strength (dB)
-50
0
50
Orientation Angle (Degrees)

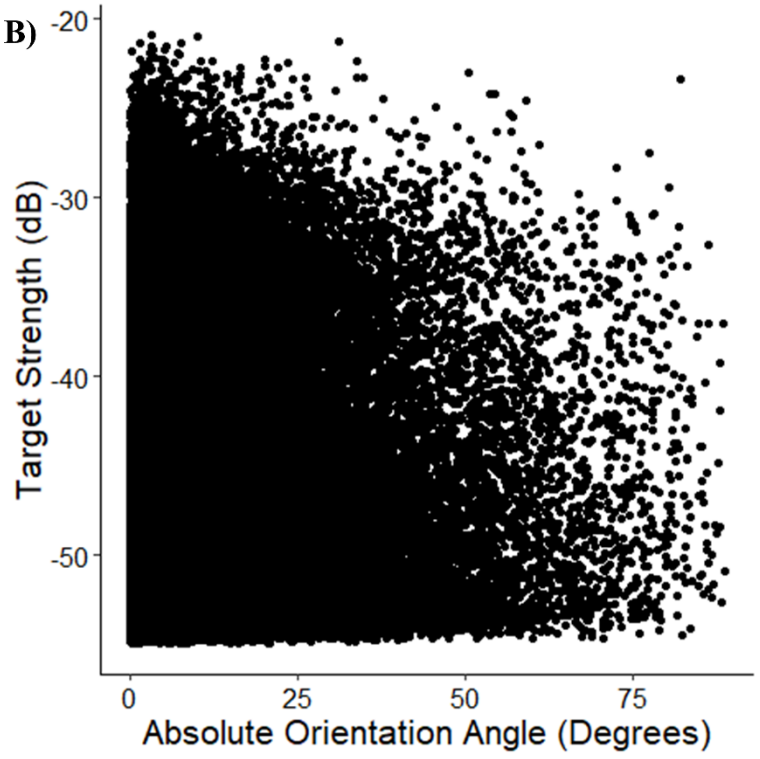

B)
-20
-30
-40
-50
Target Strength (dB)
0
25
50
75
Absolute Orientation Angle (Degrees)

Fig. S4.1. Relationships between target strength and (A) orientation angle of tracked fishes; and (B) absolute orientation angle of tracked fishes.

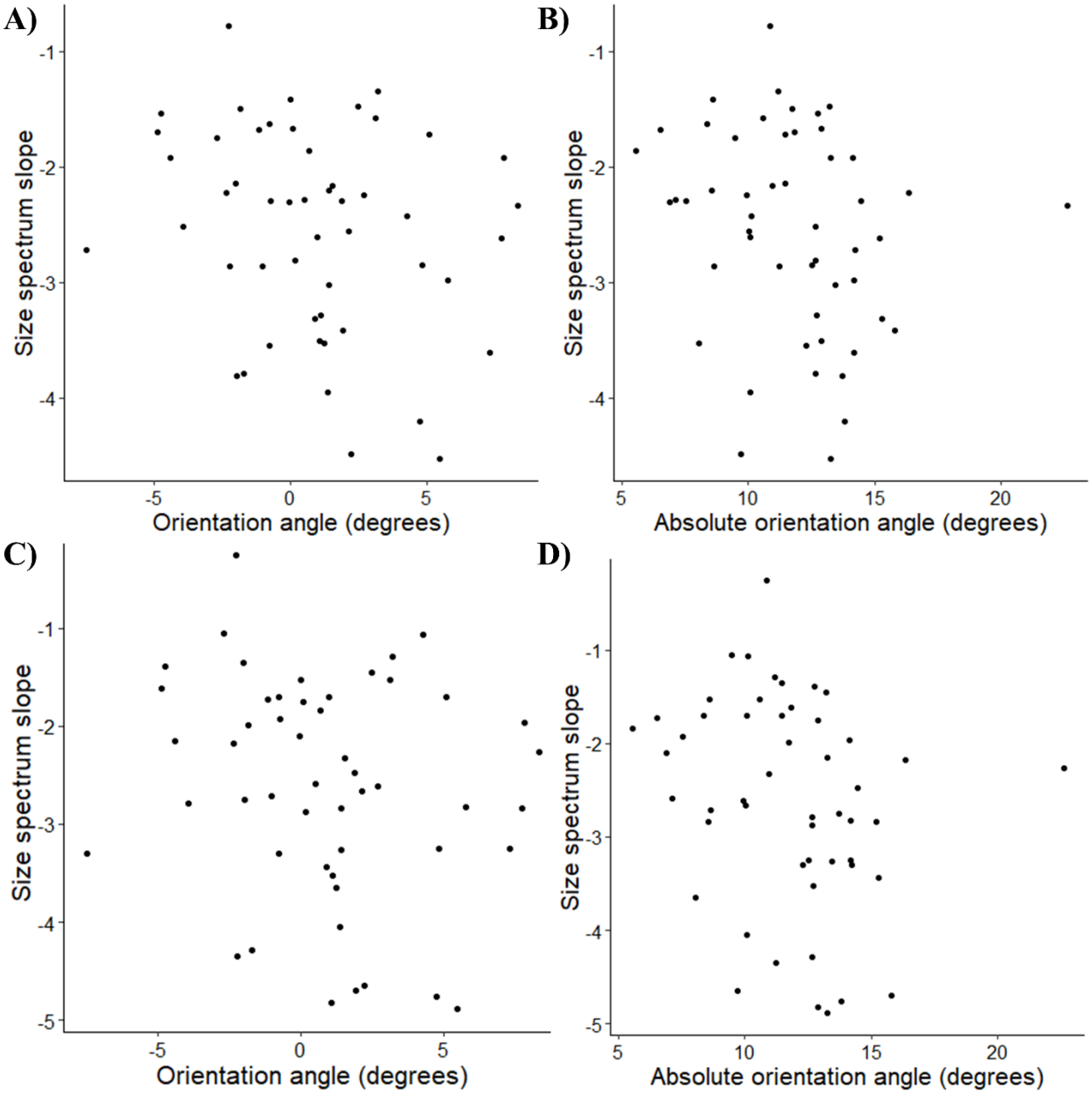


Fig. S4.2. Relationships between size spectrum slopes and orientation angle of fishes. A) size spectra slopes derived with the general target strength-length model vs. mean

orientation angle; (B) size spectra slopes derived with the general target strength-length model vs. mean absolute orientation angle; (C) size spectra slopes derived with specific target strength-length models vs. mean orientation angle; (D) size spectra slopes derived with specific target strength-length models vs. mean absolute orientation angle.

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Vita

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